Bull. Mus. natl. Hist. nat., Paris, 4e sér., **13**, 1991,
section A, nos 3-4 : 309-349.

Haemoproteus (Haemosporidia) of lizards

par Ilan PAPERNA and Irène LANDAU

Abstract. — New species of *Haemoproteus* are described and established species are redescribed from the following reptiles (geckoes and lizards) and geographical locations : *H. simondi* (Castellani & Willey, 1904), from a slide prepared by SHORTT, deposited in the GARNHAM collection, labelled "Gecko, Osmania"; *H. mackerrasi* n. sp. from *Heteronotia binoei, H. gehyrae* n. sp. from *Gehyra australis, H. oedurae* n. sp. from *Oedura castelnaui,* all from North Queensland, Australia; *H. underwoodsauri* n. sp. from *Underwoodsaurus milii,* South Australia; *H. ptyodactyli* n. sp. from *Ptyodactylus hasselquistii,* Cisjordan (West Asia); *H. tarentolae* (Parrot, 1927) from *Tarentola mauritanica,* Southwest France; *H. edomensis* n. sp. from *Agama stellio,* Cisjordan; *H. opluri* n. sp. from *Oplurus cuvieri* and *H.* cf. *opluri* from *Oplurus quadrimaculatus,* Madagascar. For each species is provided also data on the level of infection in the blood, its effect on the erythrocytes, the prevalence of multiple infections and the sex ratio among gametocytes. In all species studied there was an evident numerical disparity between macro and microgametocytes. The following criteria are proposed for differentiating reptilian species of *Haemoproteus* : shape, i.e. oval or halteridian shape, size and distribution of pigment and vacuoles; location in the erythrocytes and the form of nuclear displacement. Macro and microgametocytes of a same species may also differ in part or all of the above characteristics.

Key words. — *Haemoproteus*, Geckoes, *Agama stellio, Oplurus*, Australia, Cisjordan, France, Madagascar.

Résumé. — Neuf espèces d'*Haemoproteus* de Reptiles sont décrites ou redécrites chez les hôtes et dans les localités ci-après : *H. simondi* (Castellani & Willey, 1904), à partir d'un frottis de sang effectué par SHORTT, déposé dans la collection GARNHAM et étiqueté « Gecko Osmania »; *H. mackerrasi* n. sp. chez *Heteronotia binoei, H. gehyrae* n. sp. chez *Gehyra australis, H. oedurae* n. sp. chez *Oedura castelnaui,* tous provenant du Nord Queensland, Australie; *H. underwoodsauri* n. sp. chez *Underwoodsaurus milii,* de l'Australie du Sud; *H. ptyodactyli* n. sp. chez *Ptyodactylus hasselquistii,* de Cisjordanie (Asie de l'Ouest); *H. tarentolae* (Parrot, 1927) chez *Tarentola mauritanica,* du sud-ouest de la France; *H. edomensis* n. sp. chez *Agama stellio,* de Cisjordanie; *H. opluri* n. sp. chez *Oplurus sebae* et *H.* cf. *opluri* chez *Oplurus quadrimaculatus,* de Madagascar. Pour chaque espèce, des renseignements sur les taux des infections sanguines, l'effet du parasite sur l'érythrocyte, la prévalence des infections multiples et le sex-ratio des gamétocytes sont fournis. Dans toutes les espèces étudiées, l'inégalité numérique entre gamétocytes mâles et femelles était nette. La différenciation entre les espèces d'*Haemoproteus* repose sur les critères suivants : forme ovale ou halteridienne, taille et distribution du pigment et des vacuoles, place occupée dans l'érythrocyte et particularités du déplacement du noyau. Ces caractères varient parfois également chez les macro et microgamétocytes d'une même espèce.

Mots clefs. — *Haemoproteus*, Geckos, *Agama stellio, Oplurus,* Australie, Cisjordanie, France, Madagascar.

I. PAPERNA and I. LANDAU, *Laboratoire de Zoologie (Vers) associé du CNRS et Laboratoire de Protozoologie et Parasitologie comparée (ÉPHÉ), Muséum national d'Histoire naturelle, 61, rue Buffon, 75231 Paris, cedex 05.*
I. PAPERNA, permanent address : *Department of Animal Sciences, Faculty of Agriculture of the Hebrew University of Jerusalem, Rehovot, 76-100, Israel.*

Introduction

The taxonomic position of reptilian haemoproteids in relation to those of birds and mammals, as well as of the different species found in reptiles is poorly defined and sometimes contradicting. Most species descriptions, many of which were made prior to 1925, do not provide the details necessary for differential diagnosis and/or are inadequately illustrated. Type (or allotype) material for many of these species is either lacking, in a poor state of preservation or inadequately labelled. A further hindrance to our understanding of this group of parasites is the scant knowledge of their life history, thus far limited to one species (*H. metchnikovi* from terrapins, studied by de Giusti, Sterling & Dobrzechowski, 1973, Stirling & de Giusti, 1972, 1974). Differentiating *Haemoproteus* spp. from *Plasmodium* spp. by the absence in the former of merogony stages in circulating blood cells was a further source of confusion and controversy due to the fact that natural, chronic infections by *Plasmodium* consisting exclusively of gamonts cannot be distinguished from *Haemoproteus* infections (*Plasmodium*/*Haemoproteus* from *Agama colonorum* of Wenyon, 1909, 1915; *Plasmodium*/*Haemoproteus mesnili* from *Naja* spp. Bouet, 1909, Wenyon 1909; Macfie 1919; *Plasmodium*/*Haemoproteus gonsalezi*, Iturbe & Gonzales, 1921, Wenyon, 1926; *Plasmodium*/*Haemoproteus catenatus*, Pessoa & Cavalheiro, 1970, Telford, 1984).

In the present communication we describe seven new species of *Haemoproteus* and redescribe *H. simondi and H. tarentolae.*

Materials and methods

The material for this study was obtained from surveys of reptilian blood parasites and from slides of the collection of the Muséum national d'Histoire naturelle, Paris (*vide* MNHN). Captured geckoes and lizards were taken live to the laboratory. Blood was obtained by clipping the tip of the tail or the tip of the toe. Smears were air dried, fixed in methanol and stained for 1 h in diluted giemsa stain (0,8 % in phosphate buffer pH 7,2). Infected reptiles were kept alive in the laboratory in order to follow the course of the infection. The reptiles were maintained at an ambient temperature of 24°-28° C and fed on various insects. Blood examinations of the infected specimens were carried out at be-monthly or monthly intervals. Counts of the parasites' developmental stages were carried out per at least 1000 erythrocytes. At necropsy of the reptiles, smears as well as histological sections were prepared from the visceral organs. Smears were stained as above. Tissues were fixed in Carnoy's solution, then embedded in paraffin wax, and the prepared sections were stained by the Giemsa colophonium method. All recorded measurements are in microns.

Demonstration of development in a presumed insect vector was attempted by feeding laboratory bred *Culicoides nubeculosus, Culex pipiens molestus* (MNHN cultures) and *Phlebotomus papatasi* (obtained from Prof. J. A. Rioux, Laboratoire d'écologie médicale et de Pathologie parasitaire, Faculté de Médecine, Montpellier) on infected reptiles. Animals restrained in a wire cage were exposed to 24 h starved insects for overnight. Engorged insects, were dissected for the demonstration of oocysts 3-5 days later.

Abbreviations

a, macrogametocyte; cy, caryosome/s; i, microgametocyte; j, juvenile gametocyte; ja, juvenile macrogametocyte; ji, juvenile microgametocyte; N, Host cell nucleus; nz, nuclear zone; p, pigment; Py, accessory granule; t, trophozoite; VC, vacuole; VS, vesicle or cistern; v, RBC infected by *Pirhemocyton* virus; vc, vacuole in RBC induced by the viral infection; vf, virus "factory".

The following abbreviations are used in the text : L/W, length/width ratio; m, mean; n, sample size; RBC, erythrocytes. All measurements are in microns.

RESULTS

Haemoproteus simondi (Castellani & Willey, 1904) Shortt, 1922 (Figs. 1, 2)

Syn. : *Haemocystidium simondi* Castellani & Willey, 1904.

Two slides from the Garnham collection in the MNHN, numbered P 153 & P 154 and labelled : "241ZB, Gecko, Osmania (Shortt)" and "241ZB, Gecko, Osmania (Osmini?), (Shortt), Haemocystidium (Haemoproteus) simondi."

Redescription

Trophozoites were round, vesicular and 1,6-4,0 × 0,8-2,4 in size (figs. 1A, 2A, B). Young microgametocytes were absent on the slides.

Mature, 8-14 × 7-10 (m = 11,1 × 9,0; n = 13) microgamonts (figs. 1C, D, E, 2D, E) were round to oval (L/W 1,0-1,3; m = 1,1) and contained a foamy or distinctly vacuolated red cytoplasm with scattered grains of black pigment. Deep red, single or fragmented caryosomes were only detected in some of the microgametocytes.

Young, oval-shaped, 4,0-8,8 × 2,4-8,0 (n = 15) macrogametocytes (figs. 1B, 2B, C) contained a patchily stained blue cytoplasm with few to moderate amounts of black pigment granules and nuclear material consisting of a pale red halo with a deep red caryosome on its periphery.

Mature, 8,8-13,6 × 6,4-12,0 (m = 12,5 × 9,8; n = 13) macrogamonts (figs. 1F, G, H, 2F, G, H) were spherical or bean-shaped (L/W 1,0-1,58; m = 1,3) with a dense blue cytoplasm, a faint red nuclear zone with deep red caryosome and a prominent central vacuole. In some there was either one, same sized or several smaller additional vacuoles. Mature macrogamonts contained less and finer pigment particles.

Effect on the host cells : In gamont-infected RBCs nuclei were invariably displaced to a polar position but were otherwise unaltered. The RBC stroma expanded mainly laterally (m size of macrogamont-infected RBCs : 15,6 × 12,7, L/W 1,2, n = 9; m size of microgamont-infected RBCs : 17,4 × 12,9, L/W 1,4, n = 10; and m size of uninfected RBC's : 16,4 × 13,9, L/W 1,5, n = 11). Displacement of the nucleus and broadening of the stroma was also observed in RBCs infected by 2-4 trophozoites or young gametocytes (fig. 1B, 2A) :

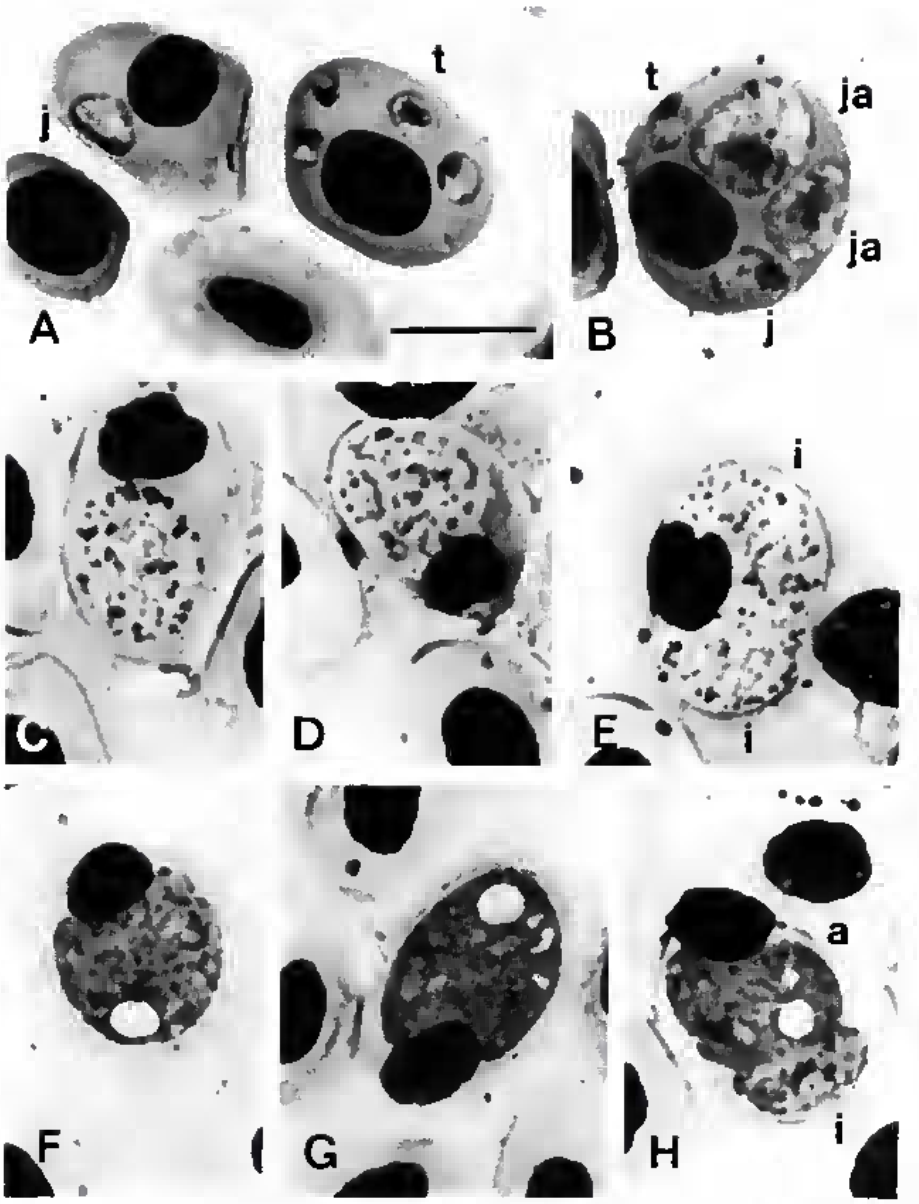


FIG. 1. — *Haemoproteus simondi* : A, trophozoites and juvenile gametocyte; B, trophozoite, juvenile gametocytes and macrogametocytes; C, D, microgametocytes; E, double infection with microgametocytes; F, G, macrogametocytes with the large vacuole; H, double infection of macro and microgametocytes. Scale = 10 μm.

trophozoite-infected RBCs of m = 15,4 × 11,4 had L/W of 1,1-1,5 (m = 1,3) while young gametocyte (< 6 × 3)-infected RBCs of m = 14,9 × 13,4 had L/W 1,0-1,3 (m = 1,1).

Level of parasitaemia, multiple infections and sex ratio : On slide P-153 mature gametocytes predominated (70 %), the other 30 % consisting of young gametocytes and trophozoites. The overall level of parasitaemia was 2,5 %, and multiple infections (fig. 1H) occurred in 21 % of the infected RBCs. Slide P-154 contained predominantly trophozoites (94 %), the rest being young gametocytes. The overall level of parasitaemia was 19 %, and the rate of multiple infections was 34 %. Trophozoites occurred in multiple infection at a rate of up to five per RBC (figs. 1A, B, 2A, B). Invasion of the RBCs was not simultaneous since

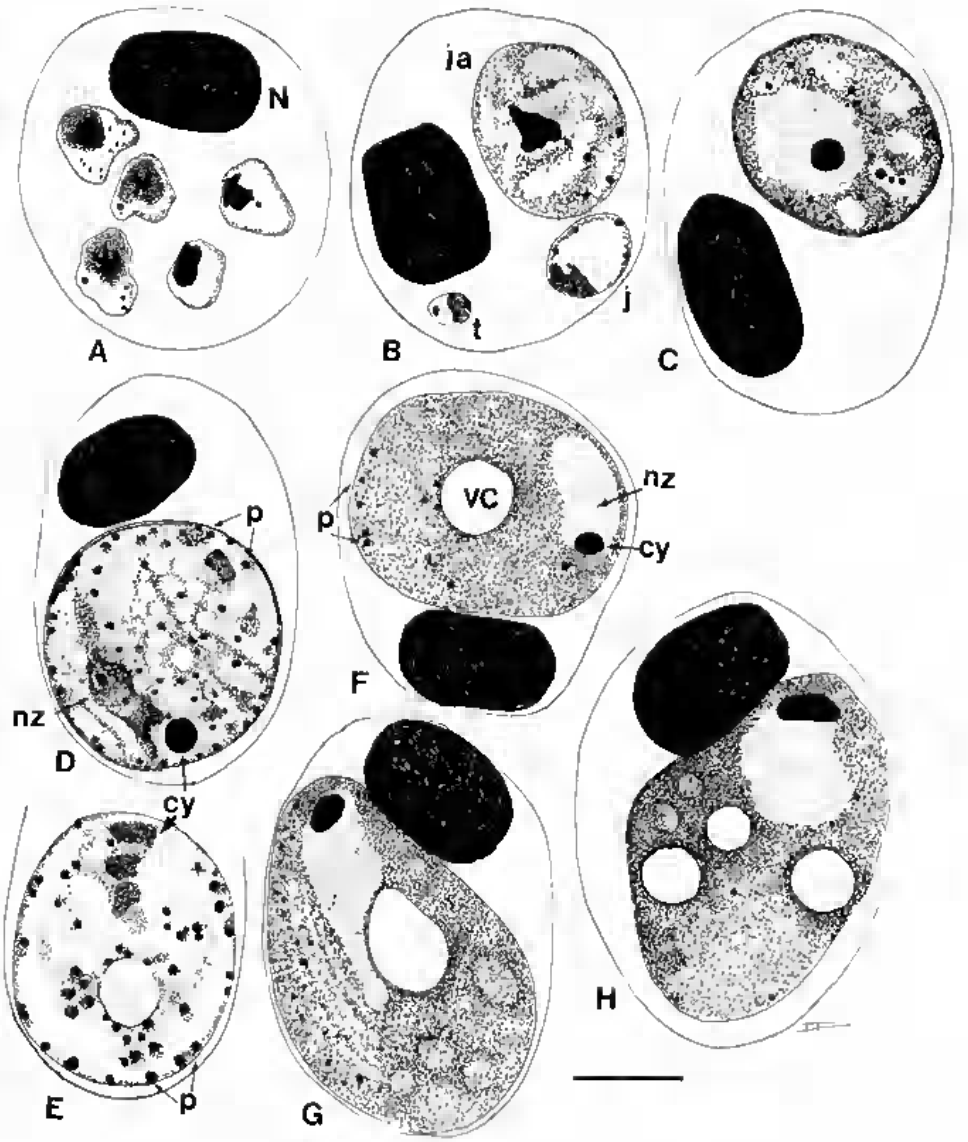


FIG. 2. — *Haemoproteus simondi* : A, trophozoites; B, trophozoites, juvenile gametocyte and macrogametocyte; C, juvenile macrogametocyte; D, E, microgametocytes; F-H, macrogametocytes. Scale = 4 µm.

these trophozoites also occurred with later stage parasites. Young macrogametocytes occurred in multiple infections at a rate of up to three per RBC. The ratio of micro to macrogametocytes was 1 : 2,1 (1 : 1,2 for mature alone).

Taxonomic evaluation

Garnham account (1966 : 952-955) and illustrations (plate LXXXVI, 2-8, facing p. 787) of *H. simondi* gametocytes is apparently based on slides P-153, P-154, referred to in his text on p. 953 as "new Indian material" from Hyderabad, in "probably *Hemidactylus brookei*". This is the same host species from which Shortt (1962) described exoerythrocytic merogony. This *Haemoproteus* seems to be conspecific with *H. dimondi* described by Castellani & Willey (1904) and later by Dobell (1910) from *Hemidactylus leschenaulti* from Ceylon. Macrogametocytes of both Indian and original Ceylonese specimens have a central large vacuole. This vacuole occurring only in the macrogametocytes is a conspicuous diagnostic characteristic of *H. simondi.*

HAEMOPROTEUS OF AUSTRALIAN GECKOES

"*Haemocystidium simondi*", described by Mackerras (1961) from four species of geckoes, *Heteronotia binoei, Gehyra variegata, Oedura tryoni* and *Phyllurus platurus*, appears to represent two or more different species : oval, rounded (from *H. binoei, G. variegata* and *P. platurus*) and halteridium-like (from *O. tryoni*). None of these are conspecific with *H. simondi* described by Castellani & Willey (1904). We identified an oval, rounded species from the *H. binoei* and *Gehyra australis* that we examined which appear to be conspecific with the ones reported by Mackerras (1961) from *H. binoei* and *G. variegata*, respectively. We also found two distinct halteridian forms, both reminiscent of the one described from *O. tryoni.*

Haemoproteus mackerrasi n. sp.

(Figs. 3, 4)

Syn. : *Haemocystidium simondi* Mackerras, 1961 of *H. binoei.*

Host : *Heteronotia binoei* Gray, 1845.

Locality : Dry woodland on the outskirts of Townsville, North Queensland (type locality), Mornington Is. in the Gulf of Carpenteria, Queensland (Mackerras, 1961).

Type specimen : On slide 145EB deposited in the MNHN.

Description

The smallest detectable trophozoites was 2,4 × 2,0 in size (fig. 3A). Young gametocytes, 5,6 × 4,8 could already be differenciated by cytoplasm staining into micro and macrogametocytes (figs. 3A, C). Some gametocytes had small vacuoles (fig. 3B). Young microgametocytes

(5,4-7,2 × 3,2-4,8) were usually rounded (L/W 1,16-2,25, m = 1,62, n = 4), with an excentric caryosome and a few fine pigment granules. Microgametocytes, 7,2-11,2 × 4,0-7,2 (m = 7,7 × 5,3 ; n = 12) (figs. 3D, E, J, K, M, 4A, D, E) were predominantly round/oval (L/W 1,0-2,2 ; m = 1,6 ; 75 % < 2, 25 % > 2) with variable density red, foamy or with variable number of small vacuoles cytoplasm and a somewhat denser red nuclear zone which contained one large (0,5-1,0), usually distinct, caryosome (fig. 4J). Pigment granules were fine and randomly scattered.

Microgametocytes exflagellated (figs. 3N, O) in heparinized blood left in a vial at room temperature (20-24° C) for 24 hours.

Young macrogametocytes, 5,4-9,6 × 4,0-8,0, were predominantly round (L/W 1,0-2,4 ; m = 1,43 ; n = 6), and contained a few pigment granules along their margins. Macrogametocytes 9,6-16,8 × 5,6-12,0 (m = 13,7 × 8,4 ; n = 12) in size were variable in shape (L/W 1,1-2,8 ; m = 1,8 ; 58 % < 2 ; 42 % > 2) (figs. 3C, E-J, L, M). In some instances macrogametocytes occupied the entire RBC cytoplasm (fig. 4K). The macrogametocyte cytoplasm stained deep blue and was without large vacuoles. A large, dense red caryosome was usually present and was located within or alongside the red nuclear zone. The pigment consisted mostly of fine granules with very few coarser grains, both randomly scattered (figs. 4B, C, E-I). Some mature macrogametocytes had undulating margins (fig. 4E).

Effect on the host cells : Infected RBCs were either only slightly enlarged or not at all. Mean size of uninfected RBCs was 18,4 × 10,8 (n = 14) ; size of infected cells ranged from 17,6-19,6 × 10,4-11,6. Heavy multiple infections had a variable effect, with some of the RBCs becoming enlarged or deformed (expanded : 19-21 × 13-17 or elongated, up to 24 × 10 (fig. 4D, H)). In most infected RBCs, including those with multiple infection, the nucleus retained its central positions, if the nucleus was displaced then it was usually laterally, and only exceptionally to a polar position (figs. 3C-F, J, M, 4D, G, H).

Prevalence of infection, multiple infections and sex ratio : In the Townsville area, infection was found in only one *H. binoei* out of 29 examined in 1986, and none in 30 examined in 1988. Mackerras (1961) reported infections in three out of seven *H. binoei* examined in Mornington Is. The level of parasitaemia in the captured gecko from Townsville was 38 %. Young and mature microgametocytes frequently formed multiple infections with other microgametocytes (in 28 % of the infected RBCs, up to five per RBC) or with macrogametocytes (1-4 per RBC, with 1-2 macrogametocytes). Multiple infections of macrogametocytes alone were rare, being found in less than in 2 % of the infected RBCs. The sex ratio was 1,4 microgametocytes per macrogametocytes.

Taxonomic evaluation

Both micro and macrogametocytes of *H. mackerrasi* are predominantly round-type *Haemoproteus*, like *H. simondi* but differ from the latter in that their macrogametocytes lack a large central vacuole and the microgametocyte pigment granules are fine rather than coarse. *H mackerrasi* is also readily differentiated from the other round species, *H. grahami* (Shortt, 1922), *H. kopki* (de Mello, 1916), and *H. tarentolae* (Parrot, 1927), which in part also form halteridian macrogametocytes and contain one or numerous conspicuous vacuoles and/or aggregated coarse pigment.

Differentiation is more difficult between gametocytes of *H. mackerrasi* and *H. gehyrae*. In the latter, microgametocytes have two endosomal, aggregated caryosomes and an accessory red granule (or "polar granule") both of which are lacking in *H. mackerrasi*. Macrogametocytes of *H. gehyrae*, unlike those of *H. mackerasi*, invariably displace the RBC nucleus to a polar position.

Haemoproteus gehyrae n. sp.
(Figs. 5, 6)

HOST : *Gehyra australis* Gray, 1845.

LOCALITY : Woodland on the outskirts of Townsville, North Queensland.

TYPE SPECIMEN : On slide 149EB deposited in the MNHN.

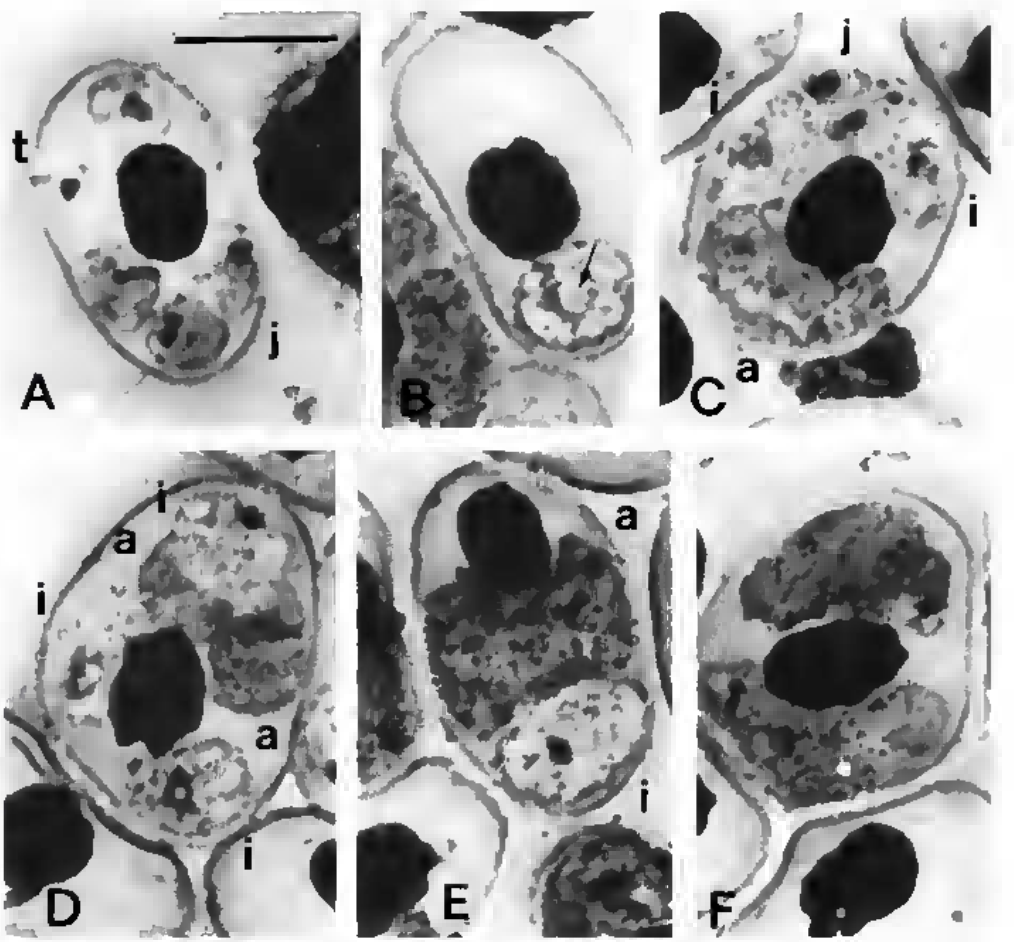
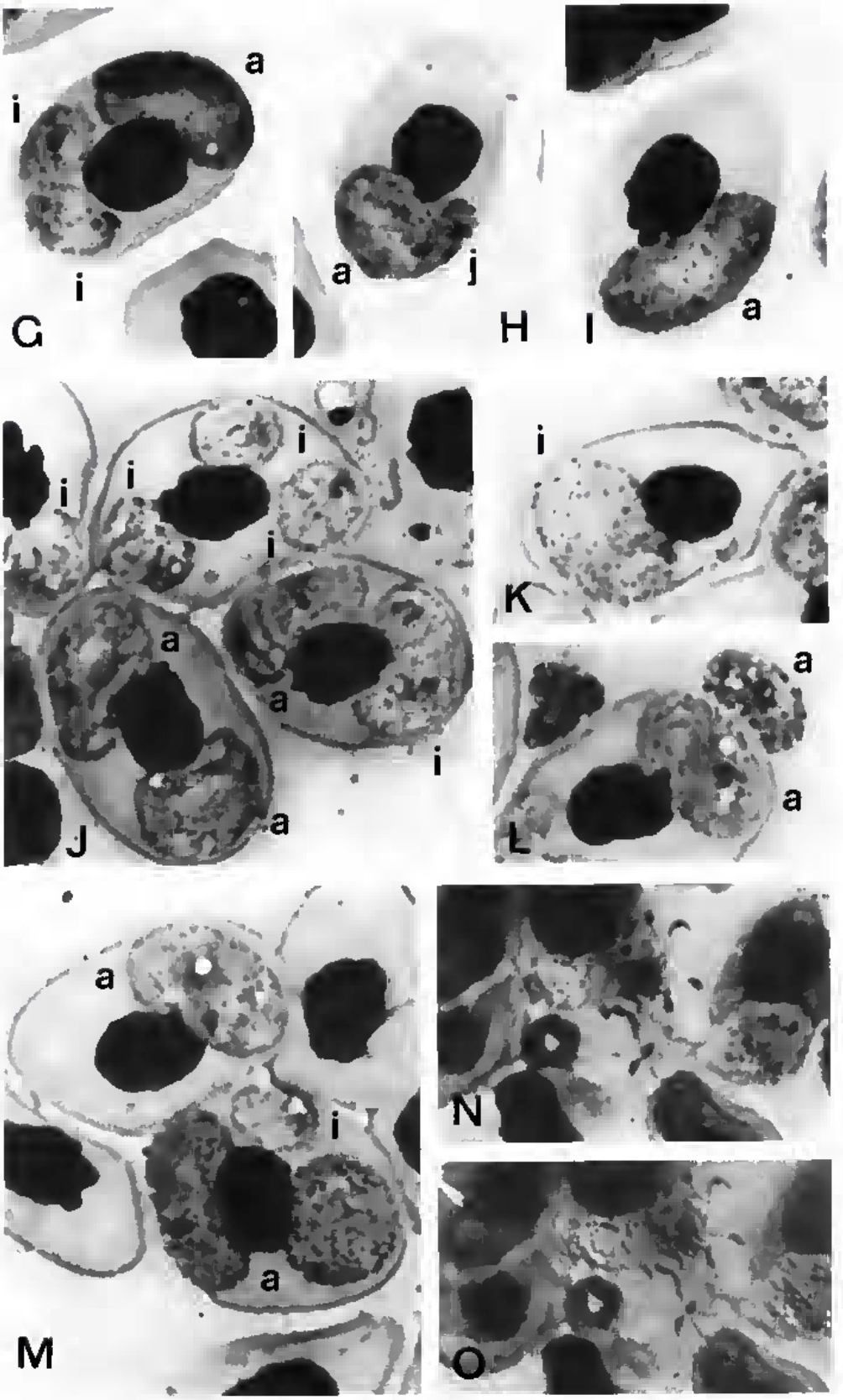


FIG. 3 — *Haemoproteus mackerrasi* n. sp. : A, mixed infection : trophozoites and juvenile gametocytes; B, young microgametocyte with central vesicle (arrow); C-M, single and multiple infections with juvenile and mature gametocytes, note (in L) evicted macrogametocytes, N, O, exflagellation of microgametocytes (N : direct illumination, O : Nomarski interference illumination) Scale = 10 µm.



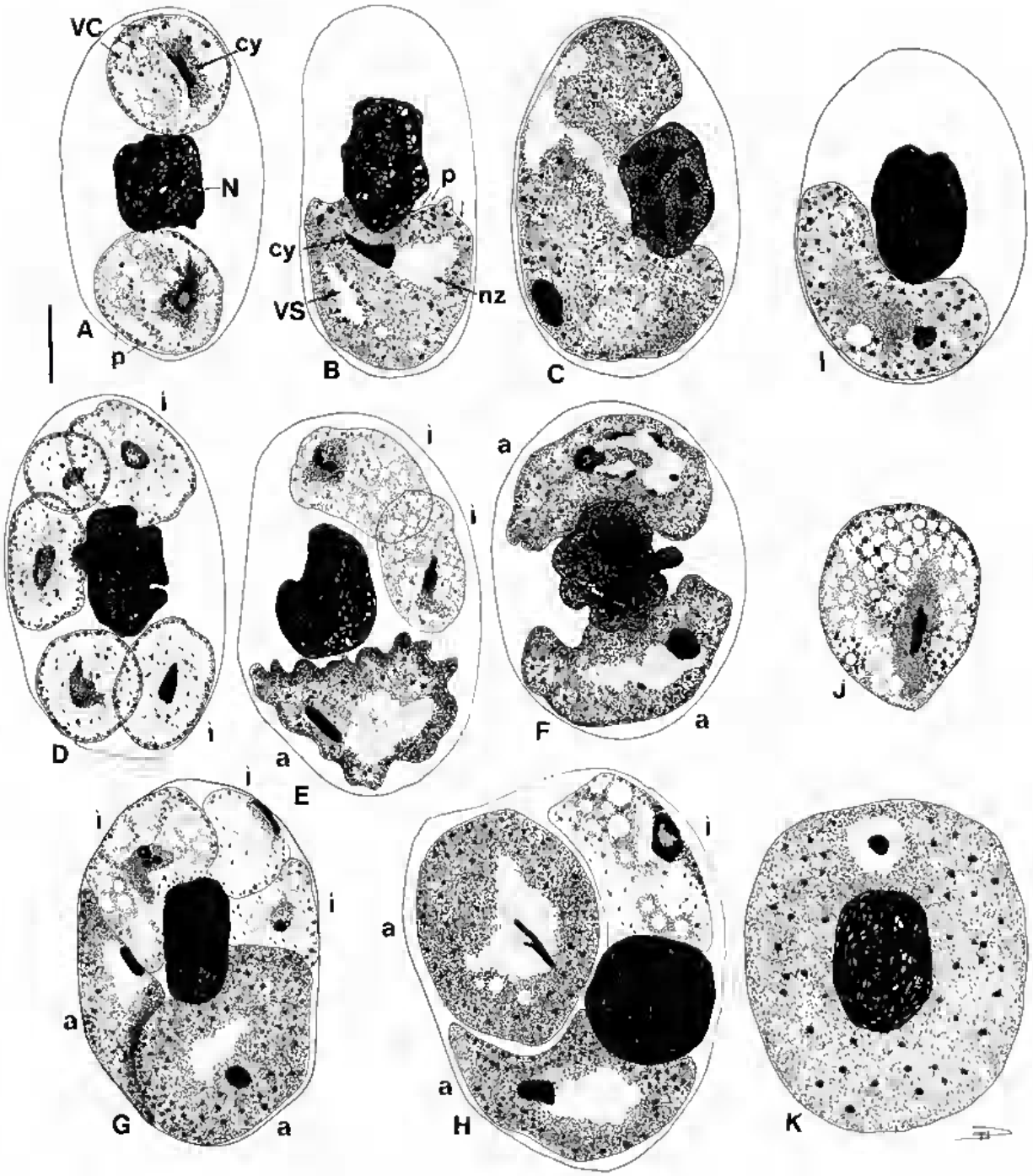


FIG. 4. — *Haemoproteus macherrasi* n. sp. : A, double microgametocyte infection ; B, C, I, macrogametocytes ; D-H, multiple infections with micro and macrogametocytes ; J, evicted microgametocyte ; K, large macrogametocyte displacing the entire RBC's cytoplasm. Scale = 4 μm.

Description

Trophozoites, 4,0-4,8 × 1,2-1,6 in size (fig. 6E) and young gametocytes, 5,0-5,5 × 2,0-4,5 (fig. 6F), were only seen in a few instances and in small numbers. Both young stages had an unstained center (extracted vacuole ?) and a peripheral zone of blue-staining cytoplasm which contained also red chromatin.

Both small and large microgametocytes (fig. 5A), 6,0-12,0 × 3,6-10,4, were round-shaped (L/W 5 % > 2,0; 95 % < 2,0; m = 1,33; n = 46). Differences between young and mature microgamonts were only in size (young : 4,8-8,0 × 3,6-5,6; n = 17; and apparently mature : 7,2-12,0 × 4,8-10,4; m = 9,8 × 7,6; n = 22). All had a faintly pink cytoplasm usually with two large, distinct deep red-staining, centrally positioned bodies — the caryosome and an "accessory granule" (figs. 6B, C, D, J). Fine pigment granules were usually evenly scattered, but sometimes aggregated. Some had faint outlines of a centrally located vacuole.

Young macrogametocytes, 5,4-9,6 × 4,0-8,0, were predominantly oval (L/W 1,1-1,7; m = 1,37; n = 10). Macrogametocytes were 9,0-14,4 × 4,0-9,6 (m = 10,5 × 7,4; n = 43) in size, with a m L/W of 1,75 (75 % round, L/W < 2, figs. 5A-E; 25 % elongated, L/W 2,0-3,1, figs. 6E, H); a few developed into long 19,2-25,6 × 4,0-7,2 (L/W 3,4-4,8) halteridia which folded over themselves in the infected RBC (figs. 5A, 6G). Macrogametocyte blue cytoplasm contained a scattered zone or bands of red nuclear material and a conspicuous or disaggregated caryosome (figs. 6A, B, I). The pigment granules were usually uniform in size and evenly scattered within the cytoplasm (figs. 5D, E). In some, pigment also aggregated into coarser granules.

Effect on the host cells : Infection caused RBCs to increase in size, distorted their shape and displaced the nucleus; most extreme changes occurred in multiple infections by three or more gametocytes. Mean size of uninfected RBCs was 16,2 × 8,7 (L/W 1,9; n = 23); infected with a single microgametocytes — 16,3 × 8,9 (L/W 1,8; n = 5); with many microgametocytes — 1,88 × 10,6 (L/W 1,7; n = 16); with one or more macrogametocytes — 1,83 × 10,9 (L/W 1,6; n = 18); and with micro and macrogametocytes — 17,6 × 9,7 (L/W1,8; n = 8). Extreme enlargement and distortions were observed in some individual cells infected with three and four microgametocytes (18 × 18; 20 × 10; 21 × 13) and also RBCs infected with one or two macrogametocytes (19 × 11,14; 20 × 12). A concurrent infection with *Pirhemocyton* caused atrophy as well as additional disfiguration of the RBC (figs. 5A, D). The m size of the RBC infected with only *Pirhemocyton*, at its latest stage (fig. 5C), was reduced to as low as 13 × 10 (L/W 1,3; n = 10). Such cells, however, were somewhat larger when being infected with *Haemoproteus* (14,6 × 9,5; L/W 1,52; n = 9) (figs. 6I, J). Macrogametocytes frequently caused displacement of the RBCs nucleus to a polar or lateral position. Single microgametocytes usually did not affect RBC nucleus' position, while in multiple infections the extent and direction of the nuclear displacement depended on the position of the gametocytes in the RBC (figs. 5A, E, 6A, C, G).

Prevalence of infection, multiple infections and sex ratio : In the Townsville area, infection was found in one out of the 19 *G. dubia* studied in 1986, and in none of the 15 studied in 1988. The infected gecko was maintained in captivity under observation from August 1986 to July 1987. The level of parasitaemia in August 1986 was 45 %, reaching 57 % in October and

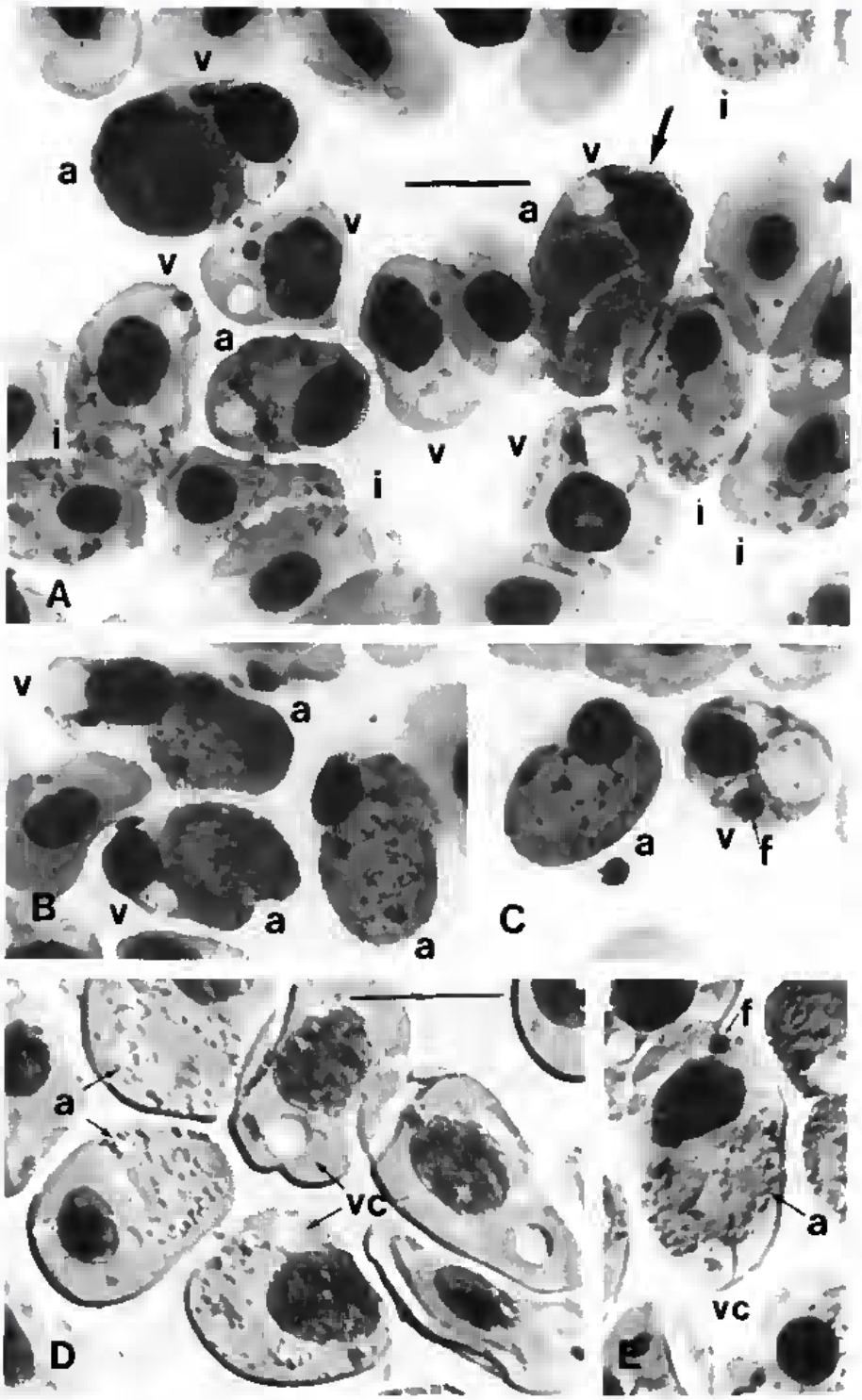


FIG. 5. — Mixed infection of *Haemoproteus gehyrae* n. sp. and *Pirhemocyton* virus : A-C, direct illumination, arrow : RBC containing long, folded macrogametocyte; D, E, Nomarski interference illumination. Scale = 10 µm.

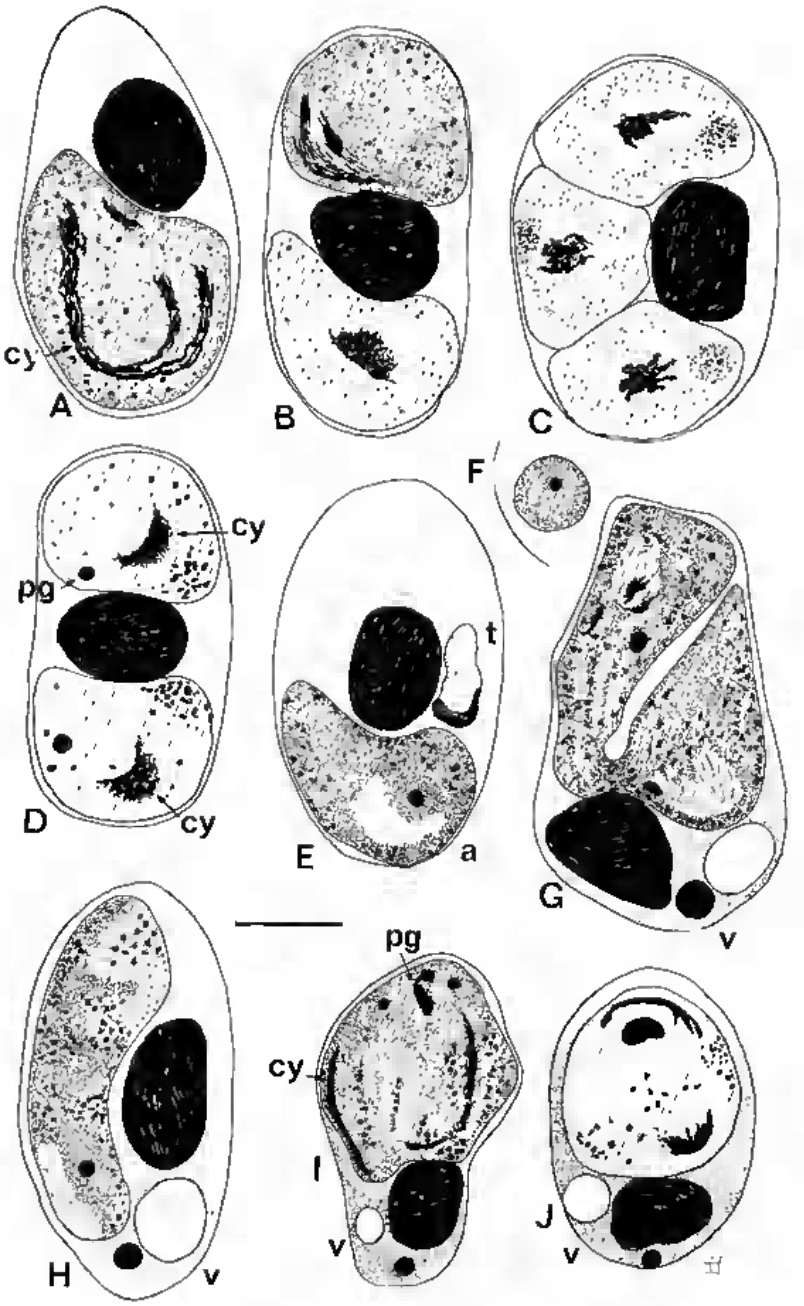


FIG. 6. — *Haemoproteus gehyrae* n. sp. : A-F, 1-3 months after host capture : A, macrogametocyte; B, micro and macrogametocytes; C, D, multiple microgametocyte infections; E, macrogametocyte and trophozoite; F, juvenile macrogametocyte; G-J, 4-5 months after host capture, infection superimposed by *Pirhemocyton* virus : G, large folded macrogametocyte; H, halteridium-like macrogametocyte; I, oval macrogametocyte; J, microgametocyte. Scale = 4 μm.

gradually declining until mid-January 1987 to 23 %. In December-January, a *Pirhemocyton* virus infection appeared in the gecko, infecting 38 % of the blood RBCs in December and 16 % by mid January. During this time, 49-60 % of the RBCs infected by *Haemoproteus* in December and 12 % in January were simultaneously infected with the virus (figs. 5A, D). The end of the viral infection in March, coincided with a sharp decline in the level of parasitaemia by *Haemoproteus*, to less than 2 %. The infection then gradually declined to below 0,7 % in July, when the gecko died. Throughout the period of observation trophozoites occurred only once, in October, when the parasitaemia was at its climax. Multiple infections with same sex and opposite sex gametocytes, as well as with trophozoites and immature gametocytes, were common (22-46 %) during the phase of high parasitaemia, and became less frequent (8-20 %), or altogether absent with the overall decline in the level of parasitaemia. Double infections were most common, while the frequency of multiple infections (3-5) particularly of microgametocytes were less common (3-8 % of the total number of multiple infections). Throughout the observed period of parasitaemia, microgametocytes outnumbered macrogametocytes. Three times however, at high parasitaemia, microgametocyte numbers came close to parity with macrogametocytes (1,02-1,2 : 1). Otherwise the disparity was on the order of 1,4-11 microgametocytes per macrogametocyte.

Taxonomic evaluation

Mackerras (1961) recorded an infection by *H. simondi* in one of 12 examined *G. variegata* from Mornington Is. in the Gulf of Carpenteria. In this habitat, however only *G. australis* is found (S. Donnellan, South Australia Museum, personal communication), and the recorded parasite might well be conspecific with the species described here.

In size and in many of its structural details *H. gehyrae* is very similar to *H. mackerrasi*. However, *H. gehyrae* microgametocytes frequently have a pair of large, deep red staining chromatin bodies (caryosome and "accessory granule"), while *H. mackerrasi* invariably contains a single chromatin body (a caryosome). In *H. gehyrae* — infected RBCs the nucleus is always displaced, frequently to a polar position, while in *H. mackerrasi* nuclear displacement is exceptional.

Gametocytes of *H. gehyrae* are indistinguishable from the plasmodiid *Billbraya australis* found in the gecko *Phyllodactylus marmoratus* in South Australia (Paperna and Landau, 1990). In this species merogony was only seen in the first three weeks following capture while in the remaining five month of follow-up, the infection consisted entirely of gamonts. In *G. australis*, during 10 months of repeated blood examinations, trophozoites were observed only once, and dividing merogony stages were never found. Data from additional infected *G. dubia* are needed for a conclusive evaluation of the relationship between the parasites of the two geckoes.

Haemoproteus oedurae n. sp.
(Figs. 7, 8)

HOST : *Oedura castelnaui* (Thominot, 1889).

LOCALITIES : Dry woodland on the outskirts of Townsville and in Fletcher View, 15 km east of Charter Towers (141 km east of Townsville) North Queensland.

TYPE SPECIMEN : On slide 153EB deposited in the MNHN.

DESCRIPTION

The smallest observable trophozoites were round, 1,2-2,0 × 0,8-1,2 in size, with an unstained center or vacuole, a peripheral zone of blue-staining cytoplasm and a red nuclear zone (figs. 8A, B, C, a, b). On-growing trophozoites, 2,4-6,4 × 0,8-4,4 in size gradually became elongated, reduced their unstained central zone and accumulated fine pigment granules (figs. 7A, B, 8A, B, C, b). Immature gametocytes, still sexually undifferentiable, 4,0-8,0 × 1,2-4,0 in size, were already assuming a halteridium form (m L/W : 3,2; n = 9). Their patchy blue-pink cytoplasm contained a large nuclear zone and a fair amount of fine granules of black pigment (figs. 7B, 8C, c, f). Small, "young" microgametocytes, 8,0-13,6 × 1,6-6,4 in size (figs. 7B, C, 8D, g, h, i), and large mature microgametocytes, 8,0-20,0 × 2,8-9,6 (figs. 7D, E, 8G, H, I, M) were predominantly halteridia like (young L/W 1,6-5,0, mean = 3,0, n = 14; mature L/W 1,2-5,5, mean = 3,1, n = 20), and located lateral to the RBC's nucleus. A few developed into round forms (L/W < 2,0 : 20 % of the young and 28 % of the mature) and occupied a polar position in the RBC (figs. 7E, F, 8F). Microgametocytes' pink cytoplasm contained a red staining nuclear zone and several scattered chromatin granules, as well as scattered fine and coarse pigment granules. The smaller microgametocytes sometimes contained one or two very large vacuoles (fig. 8j). The cytoplasm of the larger microgametocytes stained more intensely and contained one to several round (about 0,8 in diameter) vacuoles (fig. 8H).

Macrogametocytes' blue-staining cytoplasm contained a scattered, red nuclear zone, one, or exceptionally, two chromatin bodies (caryosome and accessory granule) within or at the border of the nuclear zone, and randomly dispersed, usually fine, pigment granules. Young (figs. 7C, 8E, K, d, e) as well as mature (figs. 7G-L, 8N-P) macrogametocytes were predominantly halteridium-shaped and were located alongside the RBC's nucleus (young L/W : 1,6-5,0 ; m = 3,0, n = 14 ; mature L/W : 1,3-5,5 ; m = 2,7, n = 48) ; 14 % of the young and 23 % of the mature macrogametocytes developed into a round form (L/W < 2,0) and were located in a polar position in the RBC. Presumably mature macrogametocytes, 13,6-21,6 × 3,2-11,2 (m = 18,0 × 6,8 ; n = 43) differed from young forms, 8,0-13,6 × 2,4-6,4, in that they have variable number of 0,8-1,0 in diameter vacuoles at both ends. Some of the larger macrogametocytes accumulated coarser pigment granules and exceptionally formed discrete aggregates.

Effect on the host cells : Infected RBCs with single and double gametocyte infections became enlarged, while the nucleus either remained central, was laterally displaced (figs. 7H, I,

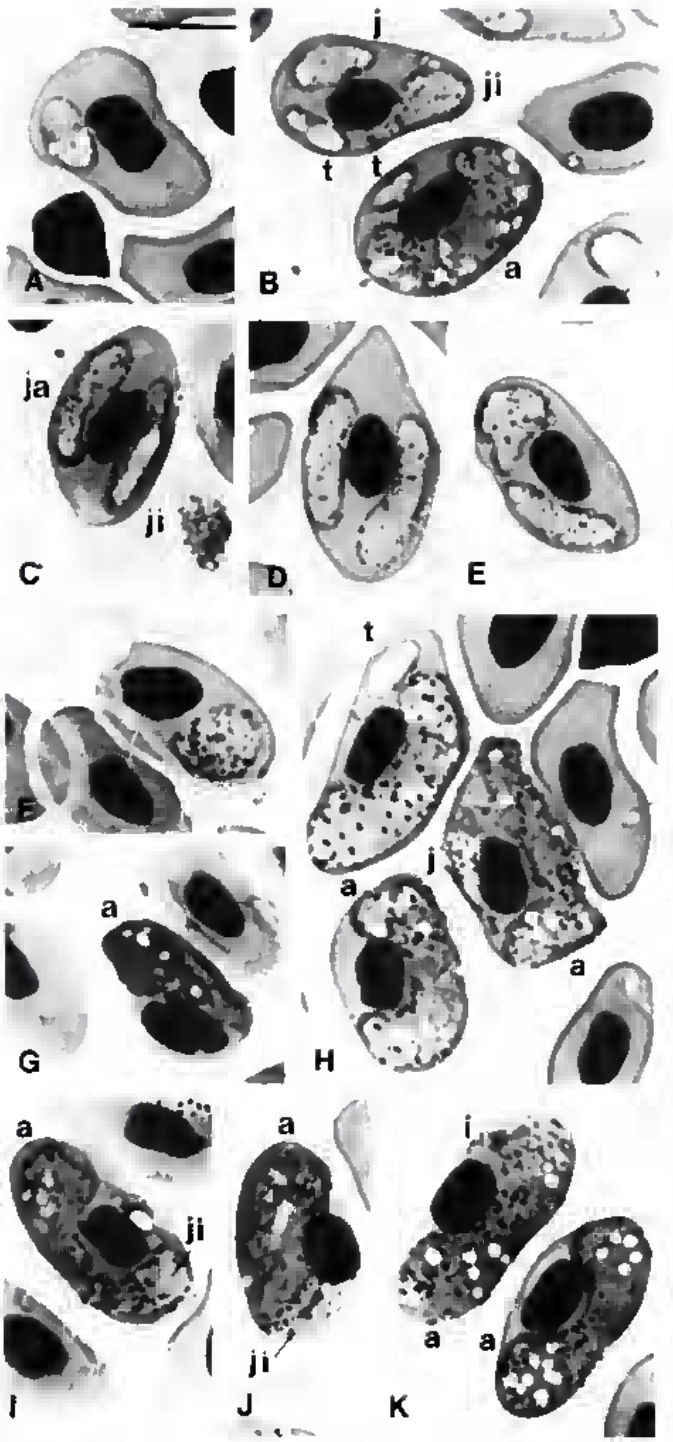


FIG. 7. — *Haemoproteus oedurae* n. sp. : A, juvenile gametocyte; B, multiple infection with trophozoites, juvenile microgametocyte and mature macrogametocyte; C, juvenile micro and macrogametocytes; D, E, microgametocytes; F, oval microgametocyte; G, sub-mature macrogametocyte; H-K, mature macrogametocytes accompanied by trophozoites and juvenile gametocytes. Scale = 10 µm.

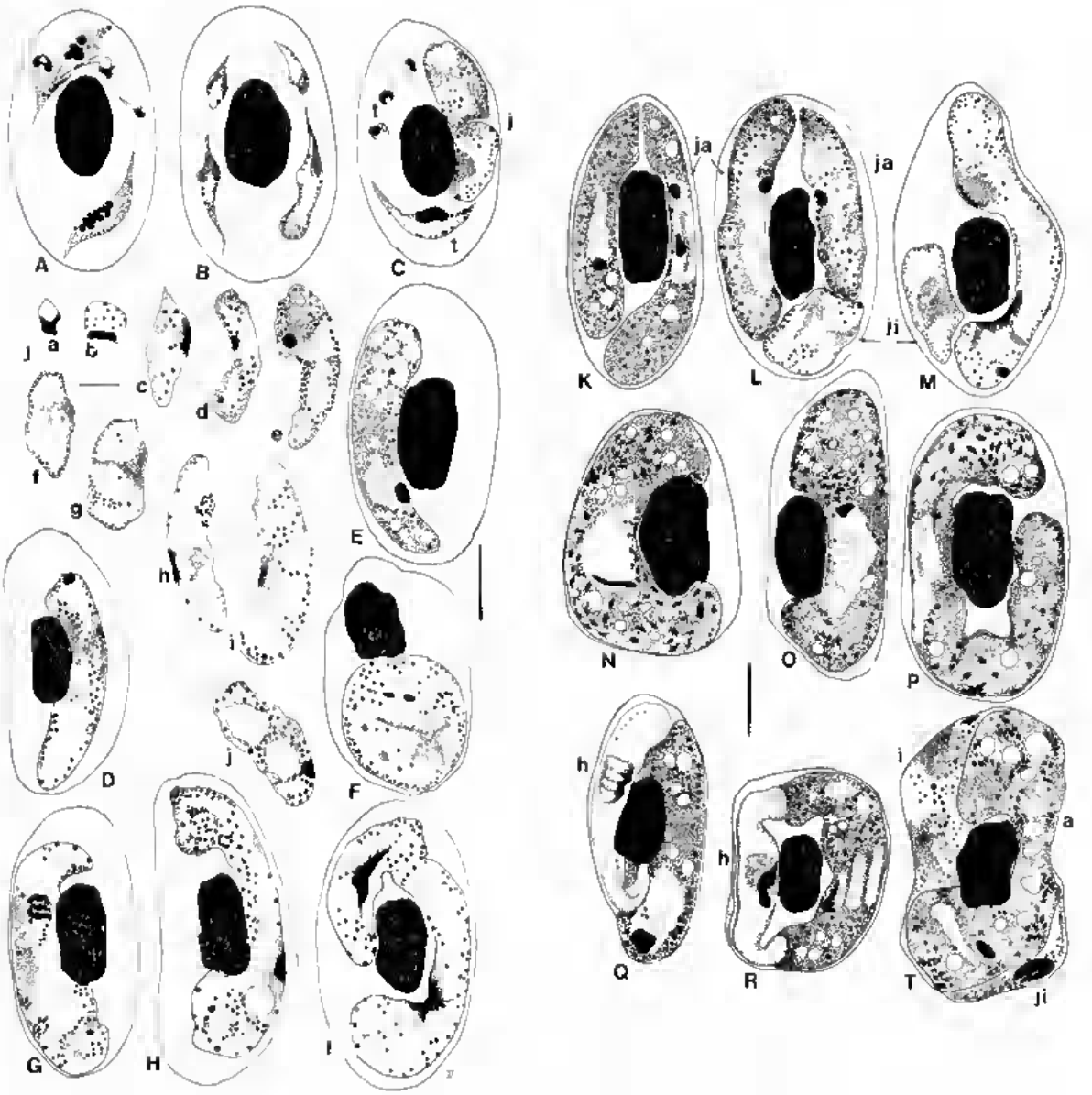


FIG. 8. — *Haemoproteus oedurae* n. sp. . A, B, trophozoites; C, trophozoites and juvenile gametocytes; D, juvenile microgametocyte; E, juvenile macrogametocyte; F-I, microgametocytes; J a-j, developmental stages from trophozoite to gametocyte : a, b, trophozoites; c-e, juvenile macrogametocytes; f-i, juvenile microgametocytes; j, juvenile microgametocyte with two centrally located vacuoles; K, L, multiple infections with juvenile micro and macrogametocytes; M, double infection of juvenile and adult microgametocytes; N-P, macrogametocytes; Q, R, mixed infection of macrogametocyte and an haemogregarine; T, multiple infection of micro and macrogametocytes. Scale A-T = 4 μm; scale a-j = 2 μm.

K, 8K, L, T), or was moved to polar position when the macrogametocyte was either round or exceptionally large and wide (figs. 7G, J). RBC also became disfigured in the few observed double infections with haemogregarines (figs. 8Q, R). Mean size of uninfected RBCs was 16,8 × 9,2 (L/W 1,8 ; n = 8) ; of RBCs infected with a single gametocyte 18-19 × 10 (L/W 1,8 ; n = 31) ; and of RBCs with two or more gametocytes 19-21 × 11-12 (L/W 1,8 ; n = 12).

Prevalence of infection, multiple infections and sex ratio : Infection was discovered in three out of the four *O. castelnaui* collected in Townsville region of Queensland. Infection was persistently low, 0,2-1,4 %, in one (an adult male) for the entire 11 month of follow-up, consisting entirely of mature gametocytes with juvenile stages occuring only rarely. Multiple infections of the RBC were scarce. In the second (subadult male), which survived only three months, parasitaemia was very high (33-68 %) with an abundance of young stages trophozoites and young gametocytes (11-52 %) and with 23-47 % multiple infections in the RBCs. The third (a young male), was negative at capture, but the infection relapsed 2-3 month later (time of onset was overlooked) and persisted for six month (till host death), reaching a peak parasitaemia of 33 % which later gradually declined to 2 %. Trophozoites and young gametocytes were abundant (32-42 %) during the first two month after the relapse of he infection, when the levels of parasitaemia were 14-33 %, and disappeared when infection later declined to 2-14 %. A high abundance of multiple infections coincided with elevated parasitaemia, comprising 11-22 % of the infected RBCs, and subsiding to 0-7 % when parasitaemia was less than 14 %. There were also sporadic occurrences of double infection with macrogametocytes and haemogregarines. Disparity between micro and macrogametocytes was evident during high as well as low-level parasitaemia. The number of macrogametocytes was equal to or slighly outnumbered that of microgametocytes (by ratios of 1,1-1,6 : 1) only for brief periods during both high and low parasitaemia. Otherwise microgametocytes predominated (1,3-15 : 1). Disparity became more extreem with the decline of the parasitaemia.

Transmission trials : Attempts to infect *Culicoides nubeculosus* in the laboratory failed, the other insects refused to feed.

Taxonomic evaluation

H. oedurae is a characteristic halteridium-like haemoproteid. It differs from other halteridian species found in saurian reptiles in the following :

H. oedurae has fine scattered pigment while *H. edomensis, H. phyllodactylli* (Shortt, 1922) and *H. ptyodactyli* have heavy, aggregated pigment. Microgametocytes of the latter species also have numerous vacuoles, rather than the few found in *H. oedurae*. *H. underwoosauri* is differentiated from *H. oedurae* by lack of vacuoles in its macrogametocyte, and in having round rather than halteridiid microgametocytes. Mackerras (1961) reports of an halteridian form of "*H. simondi*" from *Oedura tryoni*. Her data on the haemoproteids are, however, insufficient to make comparisons with other halteridian species of Australian geckoes, namely *H. oedurae* and *H. underwoodsauri*.

Haemoproteus underwoodsauri n. sp.
(Figs. 9, 10)

HOST : *Underwoodsaurus milii* (Bory de Saint-Vincent, 1825).

LOCALITY : Escarpment overlooking the Murrey river in Manum, South Australia.

TYPE SPECIMEN : Slide 150EB deposited in the MNHN.

DESCRIPTION

The very few detected trophozoites were 0,8-2,7 × 0,8-1,6 in size. Juvenile stages were also scarce. Microgametocytes (figs. 9A, B, D, E, 10D, E, H) were round to oval, 5,4-9,6 × 4,0-7,6 (L/W 1,0-1,8, n = 18). Microgametocytes from single infections were slightly smaller and stouter (m = 7,3 × 6,3; L/W 1,18; n = 9) than those from double infections with either micro or microgametocytes (m = 8,4 × 6,4; L/W 1,34; n = 9). The microgametocyte cytoplasm was stained faint red with wide, unstained enclaves (vacuoles). It contained scattered, variable size pigment granules, mostly aggregated at the periphery, and one, sometimes two or three deep red chromatin bodies (caryosome and accessory/polar granules) within or adjacent to a pale red, not well defined nuclear zone.The macrogametocytes (figs. 9C, F, G, 10A-C, F-I), 14,4-19,2 × 3,2-9,6 in size (m = 16,2 × 7,4, n = 13; with L/W of 1,8-6,0, m = 2,5), develops initially as an halteridium alongside the RBCs nucleus (fig. 10A). Fully grown, macrogametocytes occupy most of the RBC volume. In this process the RBCs nucleus remains central, completely enclosed by the parasite's cytoplasm (figs. 10G, H), or is laterally displaced (figs. 9C, F, G). In a very few instances (7 %), the macrogametocyte will expand laterally and displace the host cell nucleus to a polar position, assuming an oval/rounded shape (figs. 10C, F) (L/W 1,1-1,4). One macrogamont was exceptionally long and narrow (fig. 10I), 34,4 × 4,8; released macrogametocytes measured 24 × 8 (fig. 9G). The macrogametocyte cytoplasm stains deep blue and is void of large vacuoles. Pigment granules of variable size are scattered rather than aggregated, but, a few, may be seen concentrated around a small vacuole. A deep red caryosome is always present, adjacent to a pale red nuclear zone.

Effect on the host cells : Mean size of uninfected RBCs was 18,9 × 9,6 (n = 6; L/W 1,98). RBCs infected by single gametocytes were only slightly enlarged : m = 19,4 × 11,5; n = 10 (L/W 2,12), when infected by microgametocytes; m = 19,3 × 9,9; n = 5 (L/W 1,95), when infected by microgametocytes. Mean size of RBCs with double infections was considerably larger, 21,6 × 10,6, n = 4 (L/W 2,0) than that of uninfected RBCs.

Prevalence of infection, multiple infections and sex ratio : Infection was found in one of five *U. milii*. Blood sampled only twice, after capture and 7 days later. Level of parasitaemia was 5,9-6,0 %. Rate of double infections were 15 % and 4 % respectively. Observed micro/macrogametocytes ratios were 1,3 : 1 and 1 : 1 respectively.

Taxonomic evaluation

Macrogametocytes of *H. underwoodsauri* differ from those of other halteridian species found in saurian reptiles (*H. edomensis, H. oedurae, H. phyllodactyli, H. ptyodactyli, H. opluri*) and halteridian forms of *H. tarentolae* by their lack of vacuoles, and their round rather than halteridium-like microgametocytes.

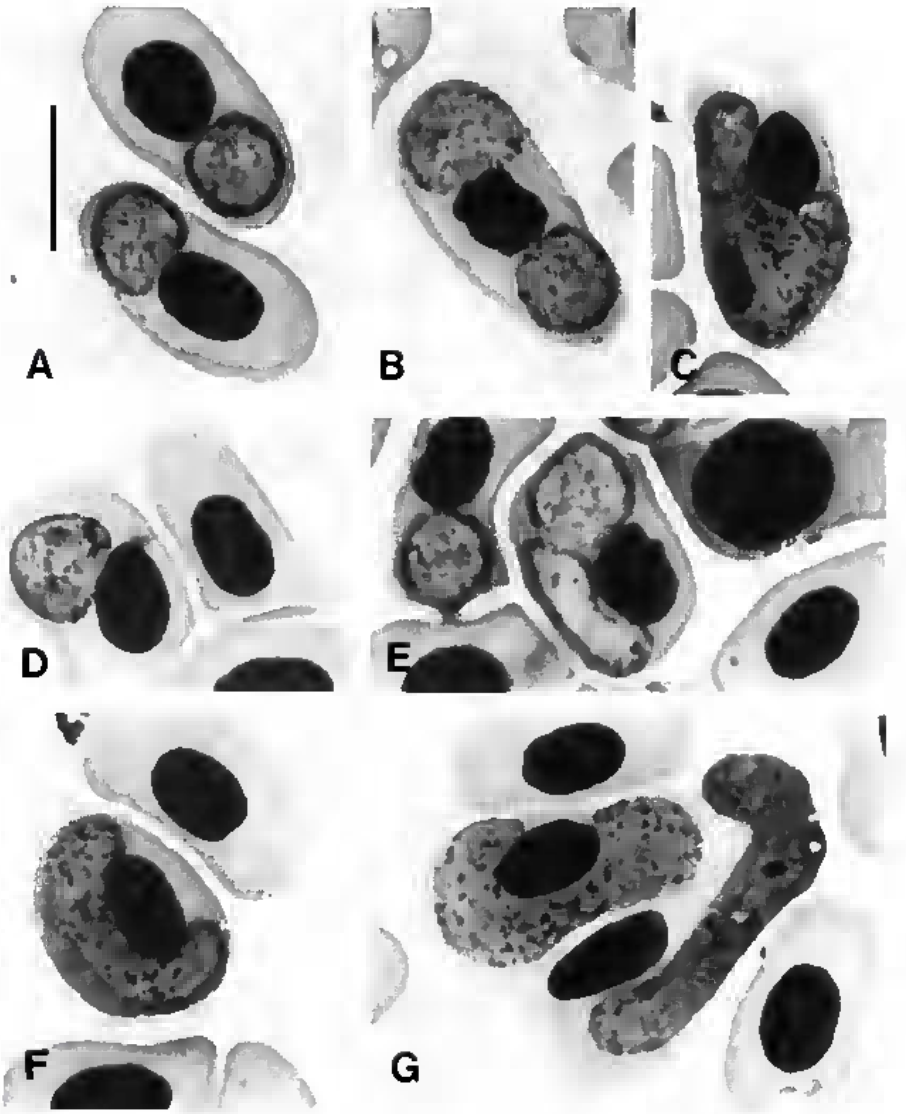


Fig. 9. — *Haemoproteus underwoodsauri* n. sp. : A, B, D, E, microgametocytes; C, F, G, macrogametocytes Scale = 10 µm

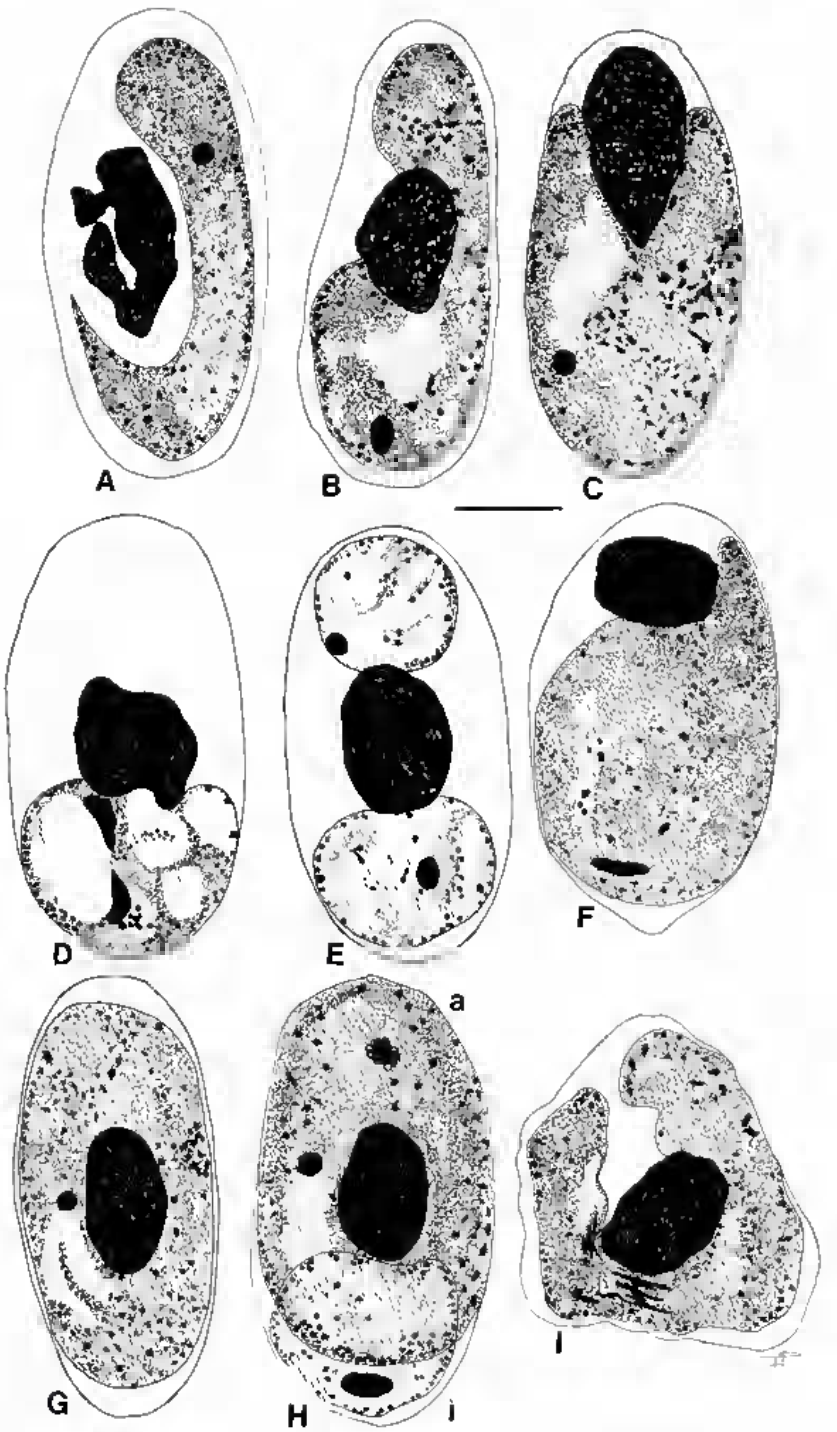


FIG. 10. — *Haemoproteus underwoodsauri* n. sp. : A, young macrogametocyte, B, C, F, G, I, macrogametocytes; D, E, microgametocytes; H, double infection of macro and microgametocytes. Scale = 4 µm.

HAEMOPROTEUS OF MEDITERRANEAN GECKOES

Haemoproteus ptyodactyli n. sp.
(Figs. 11, 12)

HOST : *Ptyodactylus hasselquistii* (Donndorf, 1789).

LOCALITY : Cave at road side near Marg' e Nag'a, Central Jordan Valley, Cisjordan.

TYPE SPECIMEN : On slide 151EB deposited in the MNHN.

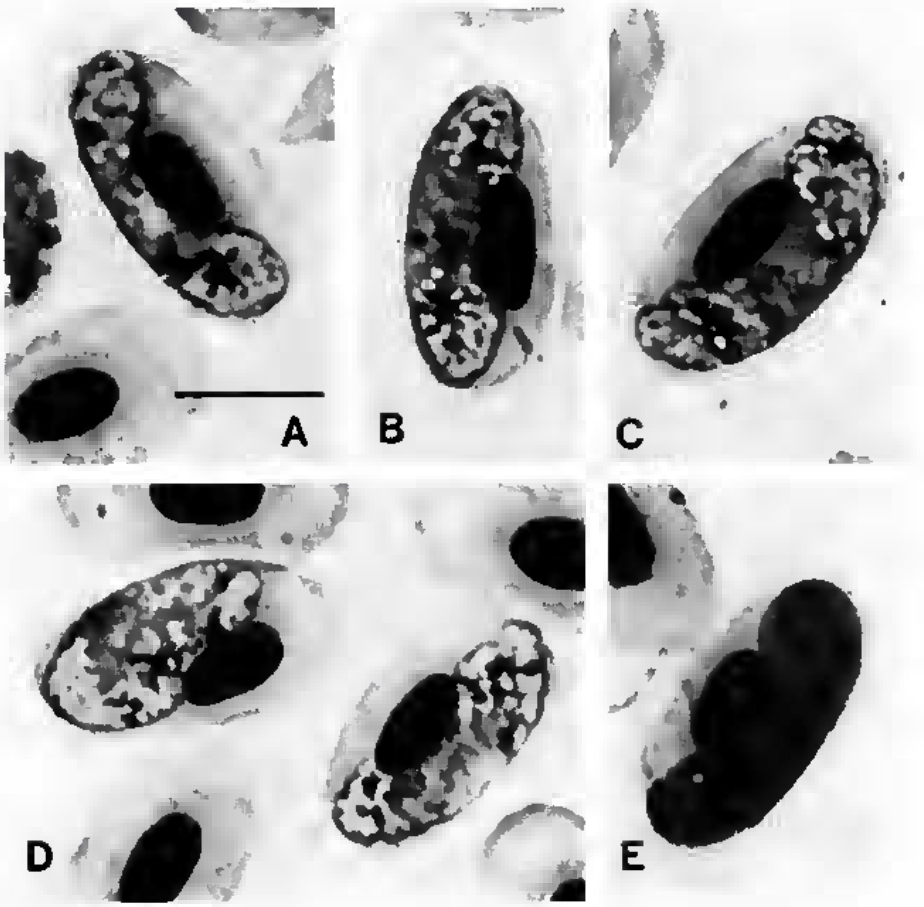


FIG. 11. — *Haemoproteus ptyodactyli* n. sp. : A-D, microgametocytes; E, macrogametocytes Scale = 10 μm.

Description

Microgametocytes were halteridium-like (figs. 11A-D, 12A-C), 16,8-22,4 × 2,4-10,0 (m = 19,6 × 7,4; n = 20), with L/W 2,1-9,0 (m = 4,2). Outlines of the pink nuclear zone were confluent with the pink cytoplasm, a caryosome was at times detectable, and an additional one or two red granules (polar granules) invariably occurred outside the nuclear zone. The cytoplasm contained many vacuoles, particularly at the distal ends of the gametocyte. Coarse, brown to black pigment was either aggregated or scattered at the two distal, heavily vacuolated zones of the cytoplasm.

Macrogametocytes were predominantly halteridia-like (figs. 11E, 12D-I), 15,2-24,0 × 3,6-6,0 (m = 19,9 × 4,8; n = 11), with L/W 3,1-6,6 (m = 3,95); about 15 % were of the rounded type (11,2-13,6 × 8,0-9,2; n = 2) with L/W of 1,4 and 1,47. The red nuclear zone with its large, round caryosome was well-demarcated in the blue-staining cytoplasm. One or two red (polar) granules invariably occurred in the cytoplasm, which also contained a few (1-4) large vacuoles and coarse black pigment which accumulated into one two discrete aggregates at the distal ends.

Effect on the host cells : RBCs infected by microgametocytes and by macrogametocytes did not diverge considerably in shape and size (m = 20,1 × 9,7; n = 18, and m = 19,2 × 9,4; n = 11, respectively) from the uninfected cells (m = 19,2 × 9,8; n = 11).

Prevalence of infection, multiple infections and sex ratio : Infection was discovered in one out of three *P. hasselquistii* captured in May 1989. Parasitaemia (1,6-2,5 %) was comprised entirely of mature gametocytes and there were no multiple infections. Microgametocytes outnumbered macrogametocytes by 1,8-9 : 1. An infection prevalence of up to 60 % is found in geckoes currently under study (since March, 1990) in the same habitat.

Transmission trials : Attempts to infect *Culicoides nubeculosus*, *C. pipiens molestus*, *Phlebotomus papatasi* and *Ph. dubosqi* in the laboratory failed.

Taxonomic evaluation

H. ptyodactyli differs from the other halteridian species : *H. underwoodsauri*, in having exclusively halteridian microgametocytes, from *H. oedurae*, and halteridian forms of *H. tarentolae*, in having their pigment aggregated around the vacuoles, and from *H. edomensis*, *H. opluri* and *H. phyllodactyli* in having numerous vacuoles at the extremities of the microgametocytes. Both micro and macrogametocytes of *H. phyllodactyli* have been reported to have one or two large vacuoles, which are localized at the extremities of the halteridian cell (Shortt, 1922); macrogametocytes of *H. ptyodactyli* contain few, variably distributed vacuoles.

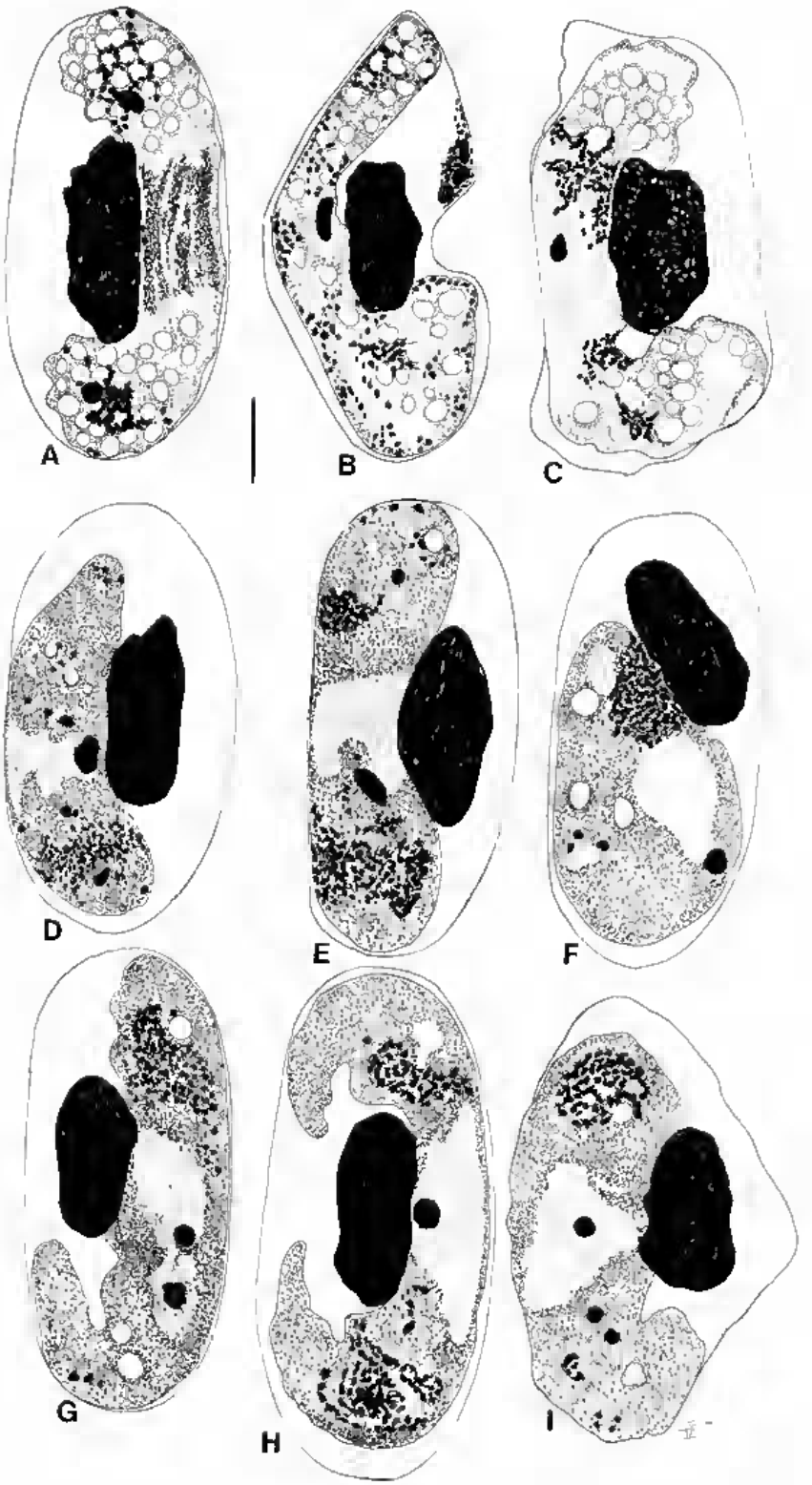


FIG. 12. — *Haemoproteus ptyodactyli* n. sp. : A-C, microgametocytes; D-I, macrogametocytes. Scale = 4 µm.

Haemoproteus tarentolae (Parrot, 1927) Riding, 1930
(Figs. 13, 14)

SYN. : *Haemocystidium tarentolae* Parrot, 1927.

HOST : *Tarentola mauritanica* (L.).

LOCALITY : Rural dwellings and vineyards on the outskirts of Banyuls-sur-Mer, South West France.

SPECIMENS : Slide t47EB deposited in the MNHN.

REDESCRIPTION

Only gametocytes were seen in the peripheral blood. The gametocyte cytoplasm had either a large 1,5-2 in diameter vacuole (figs. 13A, B, D, F, H, I, L, 14A, D, H, I, P), a large compressed cistern (figs. 14E, J), or folds, apparently marking the outlines of an emptied cistern (figs. 14K, P). These were more distinct in the macrogametocyte's intense blue-staining cytoplasm than in the microgametocytes. In other gametocytes we saw neither the vacuole nor its residues (figs. 13E, K, 14L, N, O). Microgametocytes (8,0-17,6 × 4,0-8,0; n = 36) were variable in shape (L/W 1,0-3,4, m = 1,66), being either round, and located in polar position in the RBC (figs. 14D, E) or halteridium-like, and located in a lateral position alongside or behind the RBC's nucleus (figs. 13C, D, K, 14F-H). The nuclear zone was sometimes distinct, but at other times merging with the red-staining cytoplasm. Caryosome and endosomes (polar granules) could only exceptionally be traced. Pigment material comprised coarse grains as well as scattered fine granules.

Round or oval macrogametocytes (figs. 13E-L, 14I-O), were 8,0-16,8 × 6,4-12,0 in size (n = 29) (L/W 1,0-2,2). Size and shape of the macrogametocytes varied with blood films obtained from separate hosts and examination dates and apparently represented different ages and stages of maturity (figs. 14I-L vs. M-O). Vacuoles were common in the apparently younger 8,0-12,8 × 6,4-9,6 (m = 10,6 × 8,35; n = 8) in size group, but were only seen in a few older (> 13 long) macrogametocytes. In blood films taken at later stages (over one month after capture), or from the least infected hosts, macrogametocytes were distinctly larger (11,2-16,8 × 6,4-12,0; m = 14,6 × 8,4; n = 9) (figs. 13I, K, L, 14M, N, O) than those recovered at earlier dates (9,6-15,2 × 6,4-9,6; m = 13,4 × 8,1; n = 12). These large presumably older macrogametocytes were more elongate with a mean L/W of 1,94 (1,7-2,7) than the earlier observed, < 12 µm long macrogametocytes with mean L/W of 1,7 (1,1-2,1).

Effect on the host cells : Infected RBCs were only slightly larger and expanded (m = 18,5 × 12,4; n = 35) than the uninfected cells (17,3 × 9,5; n = 14). Very large macrogametocytes or multiple infection induced further expansion and distortions in the infected RBC (20-21,5 × 8,8-12).

Prevalence of infection, multiple infections and sex ratio : Infection was found in four of the 23 *T. mauritanica*, collected on 8-11.6.89. Levels of parasitaemia in the infected geckoes at capture date were 21 %, 5,5 %, 5,0 % and 1,5 % respectively. In the last gecko, infection was

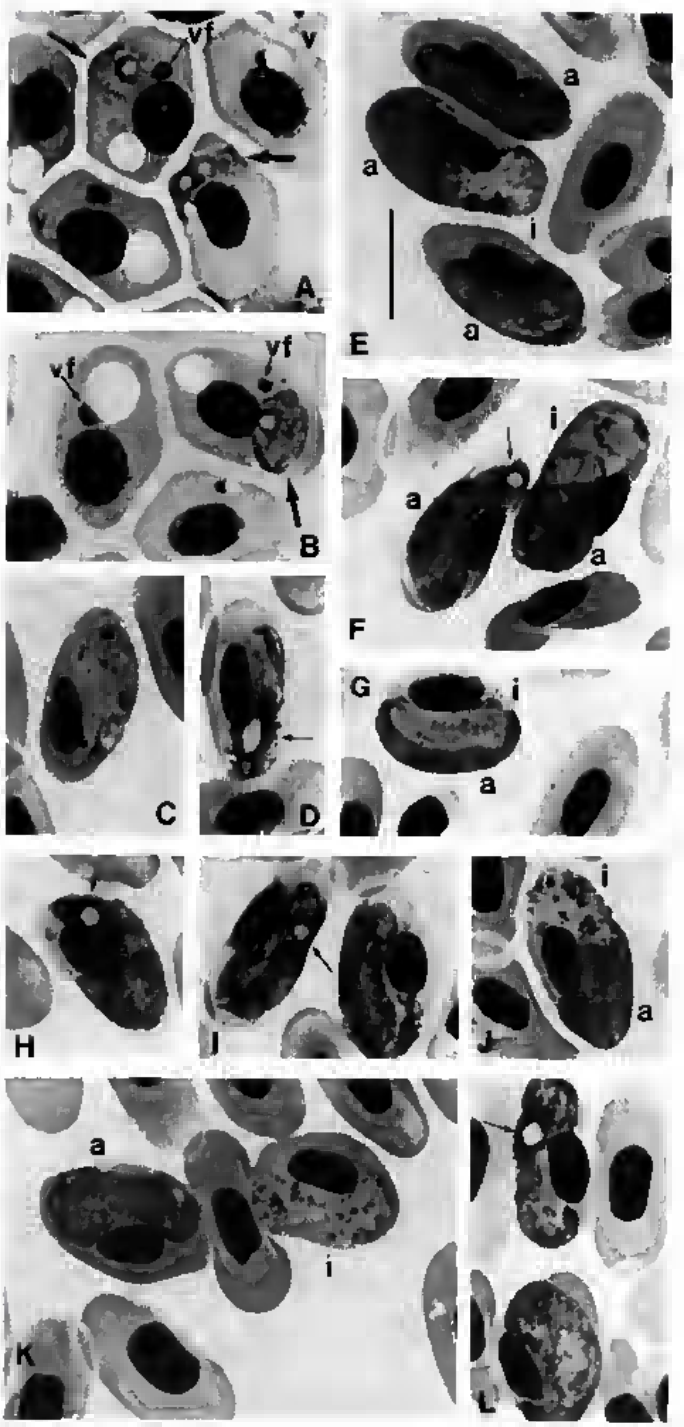


FIG. 13. — *Haemoproteus tarentolae* : The large vacuole is marked by fine arrow. A, B, juvenile macrogametocytes (bold arrows) in a concurrent infection of the RBC with a *Pirhemocyton* virus; C, D, microgametocytes; E-J, L, macrogametocytes in single infections or accompanied with a microgametocyte; K, macrogametocyte and microgametocyte. Scale = 10 µm.

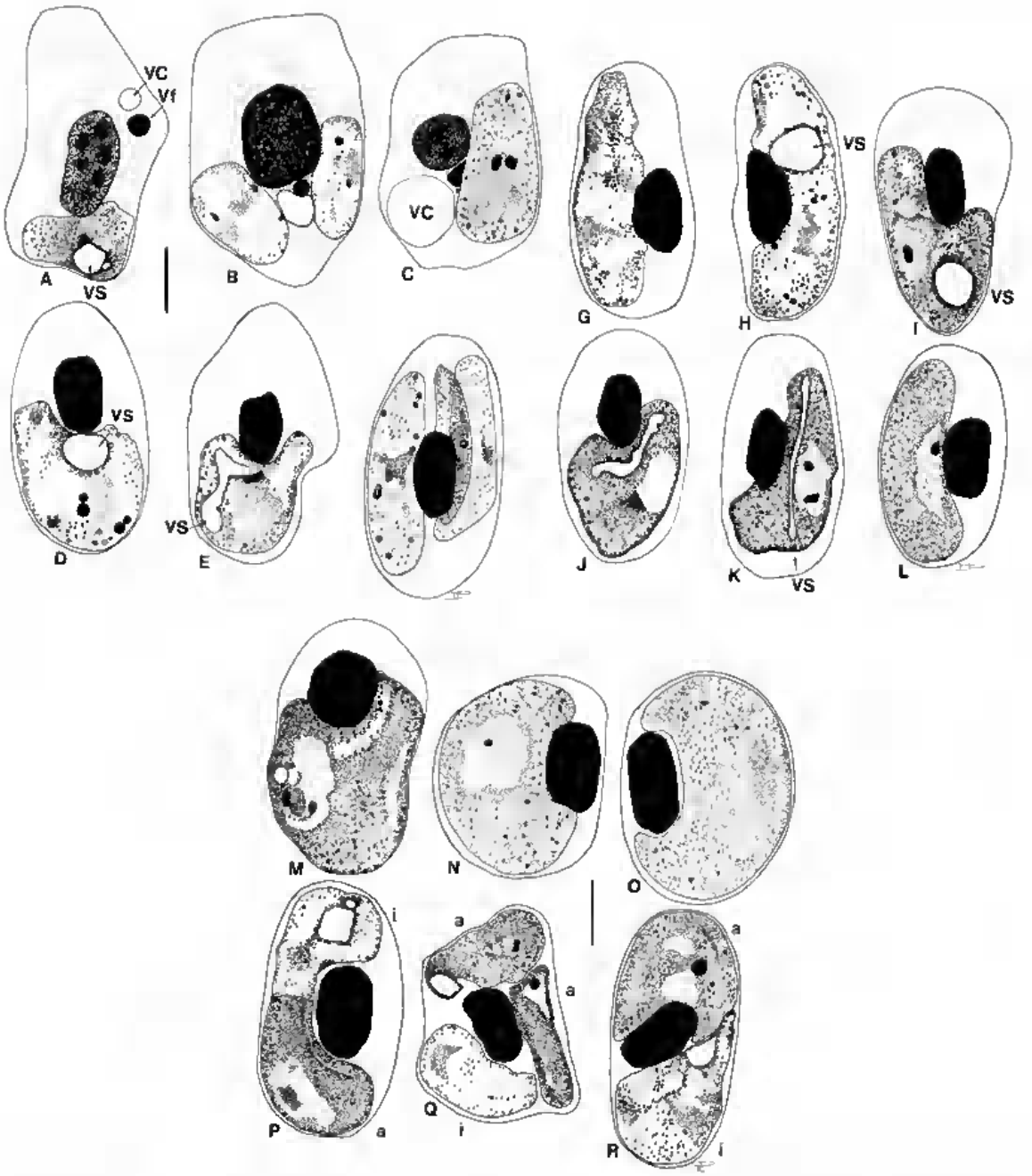


FIG. 14 — *Haemoproteus tarentolae* : A-C, juvenile gametocytes in a concurrent infection with a *Pirhemocyton* virus ; A, C, juvenile macrogametocytes; B, juvenile microgametocytes; D-H, microgametocytes; I-L, early mature magrogametocytes; M-O, old macrogametocytes; P-R, multiple micro and macrogametocyte infections of RBCs. Scale = 4 µm.

concurrent with 69 % parasitaemia with a *Pirhemocyton* virus. In this gecko (as well as in another gecko infected only with the *Pirhemocyton* virus) the infection was accompanied by a drastic proliferation of pro-erythrocytes, which suggested extreme anaemia. The parasites were mostly immature and occurred only in the virally infected cells (figs. 13A, B, 14A, B). The viral infection as well as *H. tarentolae* disappeared from the blood within one month after capture. By then blood cytology had also returned to normal. Levels of parasitaemia in the blood of the remaining three geckoes gradually declined with time. At death or necropsy three month later, the levels of parasitaemia were 4,8 %, 2,8 % and 0,05 % respectively. Multiple infections (figs. 13E, F, J, 14P, Q, R) were most frequent during high parasitaemia (13-18 %). The abundance of multiple infections progressively declined with the aging and decline of infection in the geckoes' blood (from about 5 % to 0-1 %). In the first blood examination after capture there was either parity or slight dominance (1-1,24 : 1) of microgametocytes to macrogametocytes. Thereafter and throughout the period of observation macrogametocytes outnumbered microgametocytes at a rate of 1,4 : 1 to the extreme of 72 : 1.

Transmission trials : Attempts to infect *Culicoides nubeculosus, Culex pipiens molestus* and *Phlebotomus papatasi* in the laboratory failed.

Taxonomic evaluation

Haemoproteus tarentolae described as a new species from *Tarentola annularis* found in Khartum, Sudan by Riding (1930) is in our opinion conspecific with *Haemocystidium tarentolae* described by Parrot (1927) from *Tarentola mauritanica* var. *deserti*, from Algeria. Both descriptions comprise the same parasite at different developmental stages. The vacuole characteristic of Parrot's (1927) parasites is seen in only part of the gametocytes observed in the infected blood of *T. mauritanica* from the South of France. It may not be observable when empty and disappears towards the final stages of gametocyte maturity. The latter stages correspond well with Riding's (1930) parasites. Parrot (1927) noted the occurrence of larged gametocytes in the least infected host, which presumably had been infected for a longer period of time, a phenomenon we observed in our geckoes as well. He also notes the above — mentioned dominance of macrogametocytes in the infected geckoes.

HAEMOPROTEUS OF AGAMID LIZARDS

Haemoproteus edomensis n. sp.
(Figs. 15, 16)

Host : *Agama stellio* Hasselquist and Linn., 1757.

Locality : Maaleh Edomim, 6 km east of Jerusalem, semi-desert, open rocky habitat, Cisjordan.

Type specimen : On slide 146EB deposited in the MNHN.

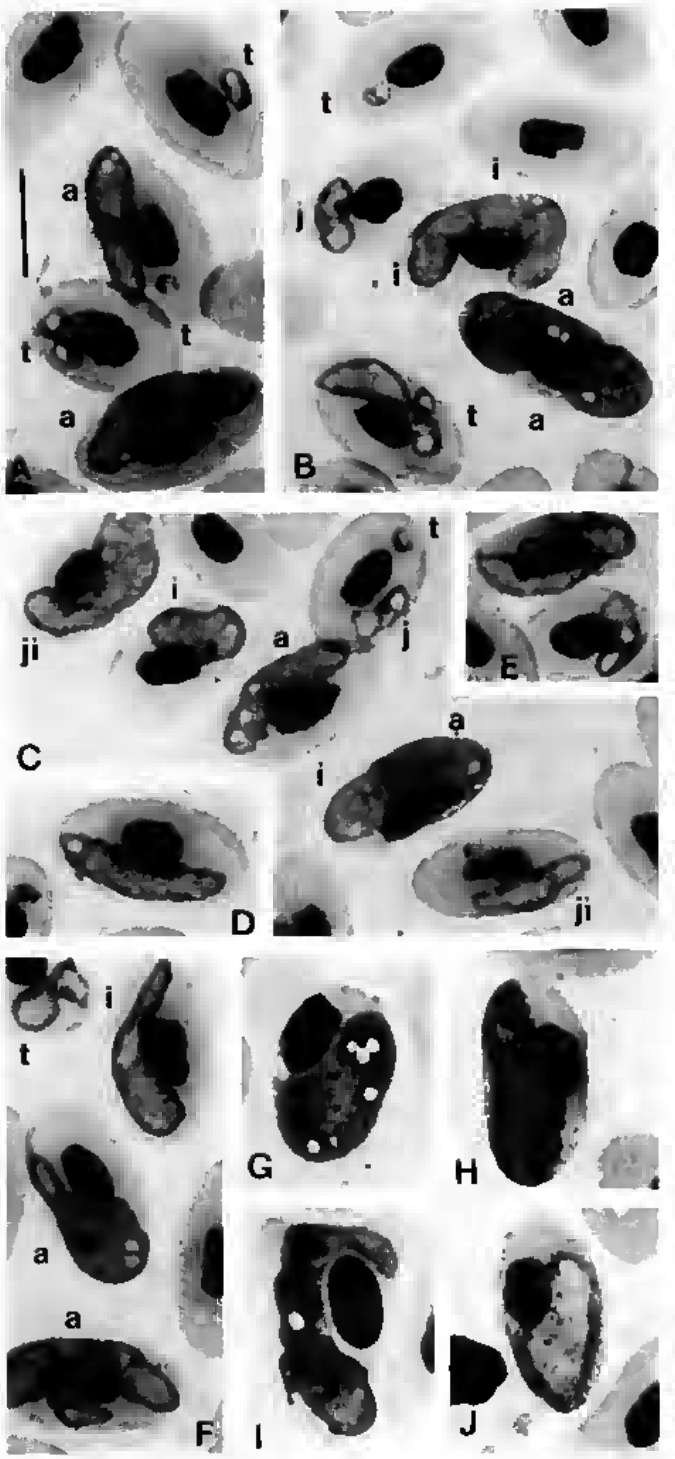


FIG. 15. — *Haemoproteus edomensis* n. sp. : A-F, single and multiple infections with trophozoites, juvenile and premature gametocytes seen during heavy parasitaemia (29-32 %); G-J, gametocytes seen in blood at low parasitaemia (< 4 %); G, H, mature large macrogametocytes; I, multiple macrogametocyte infection; J, mature, large microgametocyte. Scale = 10 µm.

Description

Observed trophozoites were round, 1,6 × 1,6 to 2,4 × 1,2-1,6 in size, usually with an unstained center and a peripheral zone of blue-staining cytoplasm, a red-staining nuclear zone and a few pigment granules (figs. 15A, B, C, 16A). On-growing trophozoites, 4,0-5,4 × 1,6-3,2 in size, gradually assumed an elongated halteridium shape (L/W 1,7-2,3) (figs. 16B, a-c) while some maintained a rounded form (L/W 1,0-1,6) (figs. 15B, C).

Mature microgametocytes were not readily distinguishable from the immature ones. Within the observed size range of 4,8-17,6 × 2,4-11,2 (figs. 15B, C, E, F) the larger, 9,6-17,6 × 3,2-11,2 (m = 13,0 × 6,2; n = 26), presumably mature microgametocytes (figs. 15J, 16K-M) contained appreciable amounts of scattered pigment and one to several deep-red

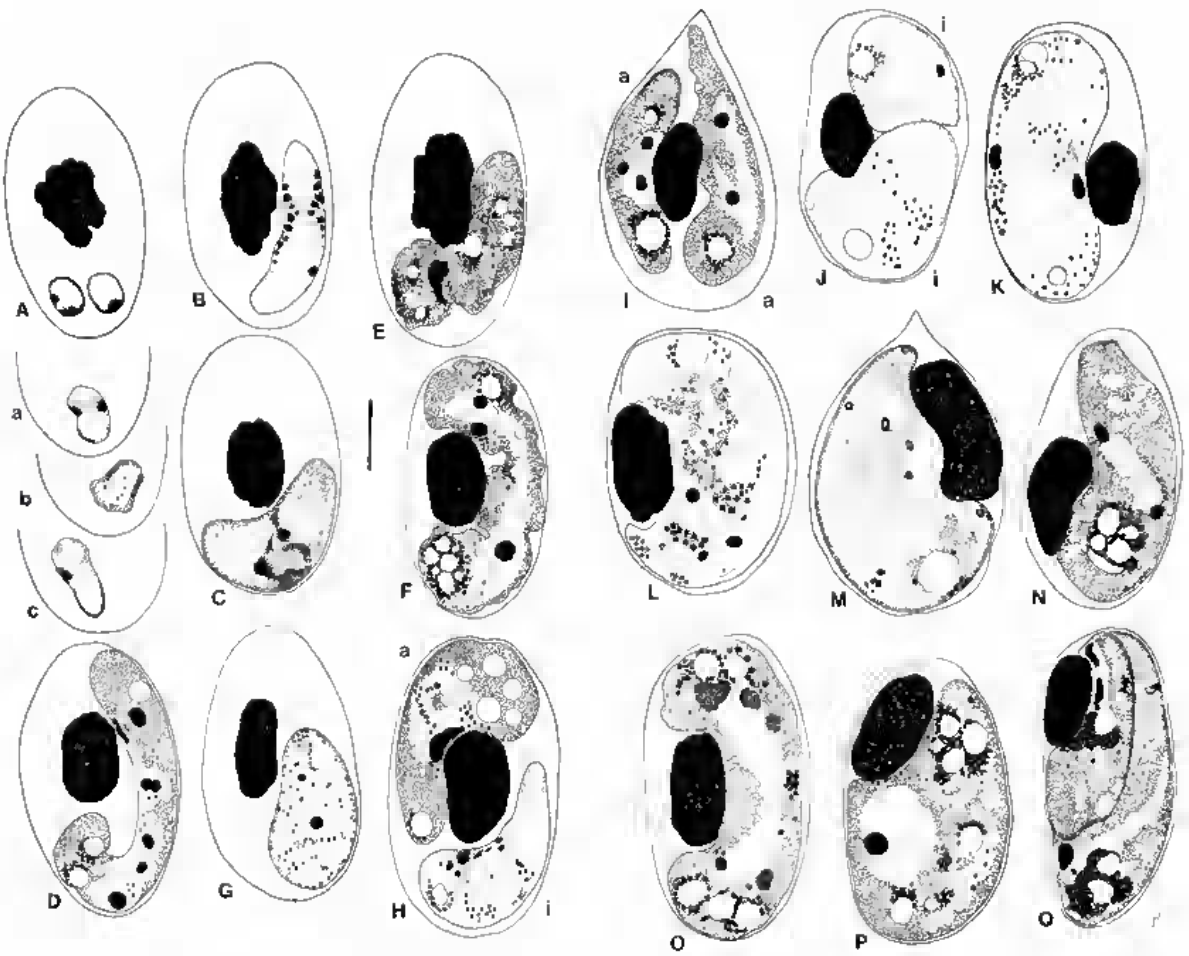


Fig. 16. — *Haemoproteus edomensis* n. sp. : A, a-c, trophozoites; B, juvenile (micro-?) gametocyte; C, D, juvenile macrogametocytes; E, F, mature macrogametocytes; G, premature microgametocyte; H-J, double infections with gametocytes; K-M, mature, large microgametocytes; N-P, mature, large macrogametocytes; Q, double infection with mature macrogametocytes. Scale = 4 μm.

staining discrete bodies or scattered aggregates of chromatin (caryosomes) in their light pink cytoplasm (figs. 16K, L). A few large microgametocytes stained uniformly deep red (figs. 15J, 16K, M). Some had one or several small vacuoles. Fifty eight percent of adult microgametocytes were elongated halteridia (L/W > 2,0 (2,0-5,2)), located laterally in the RBC, alongside the nucleus (figs. 15B, F, 16K-M), while 42 % were rounded (spherical) (L/W < 2,0 (1,1-1,9)), located at a polar end of the RBC (fig. 15C). Total L/W for all seemingly mature microgametocytes was 2,18, compared with L/W = 1,72 for juveniles, 6,4-12,0 × 2,4-8,8 (m = 10,3 × 4,8; n = 16) in size. Among the latter, 50 % were elongated and 50 % rounded (figs. 15B,C,F, 16G,H, J).

Mature macrogametocytes (12,0-20,8 × 3,2-8,8; m = 15,0 × 6,0; n = 38) occurred predominantly as halteridia (85 %), alongside the RBC's nucleus, with a L/W of 2,0-4,4 (m = 2,9; n = 32) (figs. 15F, I); some had undulating margins (figs. 15H, 16E, F). The remaining 15 % were rounded, with L/W 1,0-2,0 (m = 1,63, n = 6) and located in a polar position (figs. 15B, C, 16P, Q). Macrogametocytes' blue-staining cytoplasm contained a well-defined red-staining nuclear zone, with one or two adjunct deep red-stained caryosomes. Additional scattered or aggregated deep red stained chromatin also occurred within the nuclear zone. In the cytoplasm the dark pigment accumulated mainly around one of several large (0,4-1,0 diameter) vacuoles situated usually on one or both ends of the macrogametocyte (figs. 16N-Q). In the largest macrogametocytes (long axis > 17) (figs. 15G, H, 16P, Q) the pigment precipitated into heavy, coarse, brown particles, in the smaller ones (< 17 long axis) the pigment material was finer and more dispersed (figs. 15B, C, F, 16H, N).

Young macrogametocytes 7,2-12,0 × 2,4-8,8 (m = 9,4 × 5,0; n = 17) had fewer or altogether lacked large vacuoles, and their pigment was either scattered or beginning to aggregate. Over half (58 %) were halteridians, located alongside the nucleus, the rest were round, in a polar position (overall L/W 1,0-3,3; m = 2,1; n = 17) (figs. 15C, D, F, 16C-E, H, I).

Effect on the host cells : Infected RBCs were larger than uninfected ones. Mean size of RBCs infected with mature microgamonts was 17,0 × 10,3 (L/W 1,65; n = 26), with mature macrogamonts 17,5 × 9,4 (L/W1,61; n = 38) and with double, multiple infections 19,0 × 11,0 (L/W 1,68; n = 10). Uninfected RBCs were 16,2 × 9,2 (L/W 1,88; n = 10). Displacement of the nucleus occurred in only a few of the infected RBCs, most notably in double-infected cells.

Prevalence of infection, multiple infections and sex ratio : Infection was recovered in one out of 3 *Agama stellio* collected in March 1986 and in one out of five lizards collected in November 1988. In the first lizard, level of parasitaemia remained high (30-32 %) from the time of capture till death, 60 days later. Infection was predominantly by young stages — trophozoites (18-30 %) and young gametocytes (38-56 %), with 19-25 % of the infected RBCs having multiple infection. In the second lizard, the level of parasitaemia was initially very low (0,6 %) but it gradually increased and three months later, reached 3 %. It then remained in the range of 1-4 % untill the lizard's necropsy eight month after capture. Throughout this period trophozoites and early gametocytes were consistently present and comprised 20-75 % of the parasites seen in the RBCs. Most observed multiple infections (comprising 2,5-16 % of the infected RBCs) consisted predominantly of trophozoites and immature gametocytes. In spite of finding trophozoites in blood examined at the time of necropsy, exoerythrocytic stages were not found in all examined visceral organs (liver, spleen, kidneys, lungs, brain). Macrogameto-

cytes consistently outnumbered microgametocytes in both infected lizards throughout the observation period at rates ranging from 1,3 to 38 : 1.

Transmission trials : Attempts to infect in the laboratory *Culicoides nubeculosus*, *Phlebotomus papatasi* and *Culex pipiens molestus* failed.

Taxonomic evaluation

Heavy aggregated pigment around the large vacuoles as seen in *H. edomensis* macrogametocytes has been only observed in the other reptilian species *H. kopki* de Mello, 1916 and *H. phyllodactyli* Shortt, 1922; in the former this characteristic has only been observed in the microgametocyte, while in the latter in both sex gametocytes. In *H. edomensis* the pigment aggregates only in the macrogametocyte. *H. phyllodactyli* has been described as invariably having two vacuoles at polar positions, surrounded by the aggregated pigment (Shortt, 1922). In *H. edomensis* the number of vacuoles and their location in the cytoplasm is variable. *H. grahami* Shortt, 1922, the only other described species from agamid lizards has scattered pigment in both type gametocytes. *H. grahami* has been recorded in *A. nupta* from west-north Iran (Shortt, 1922), in *A. nupta* from west Pakistan (Telford, 1984) and in *A. caucasica*, *A. lehmanni* and *A. erythrogaster* from Turkmenistan and Uzbekistan SSR (Bogdanov, Markov & Radchenko, 1970; Ovezmukhamedov, 1987).

There are several brief reports of *Haemoproteus* sp. infections in African *Agama* lizards : in *A. agama* from Nigeria (Macfie, 1914), in *A. agama* in Liberia (Bray, 1959) and in *A. cyanogaster* from Uganda (Ball, 1967). None of these *Haemoproteus* have the characteristic aggregated pigment seen in *H. edomensis* macrogametocytes. *H. agamae* Wenyon, 1909 described from *A. colonorum* (syn. of *A. agama*) found in Bakher-el-Ghazal was later (Wenyon, 1915) reidentified as a species of *Plasmodium*.

HAEMOPROTEUS FROM LIZARDS FROM MADAGASCAR

Haemoproteus opluri n. sp.
(Figs. 17, 18)

Host : *Oplurus cuvieri* (Gray, 1831).

Locality : Majunga (type locality, slides 234LL, 236LL) and Belo sur Tsiribihina (slides 37LL), Madagascar.

Type specimen : On slide 234LL, deposited in the MNHN.

Description

Blood smears only contained fully-differentiated micro and macrogametocytes. Parasites obtained from lizards in Majunga (234LL, 236LL) were larger than those found in the lizard from Belo sur Tsiribihina (37LL). The latter also differed in some cytological details.

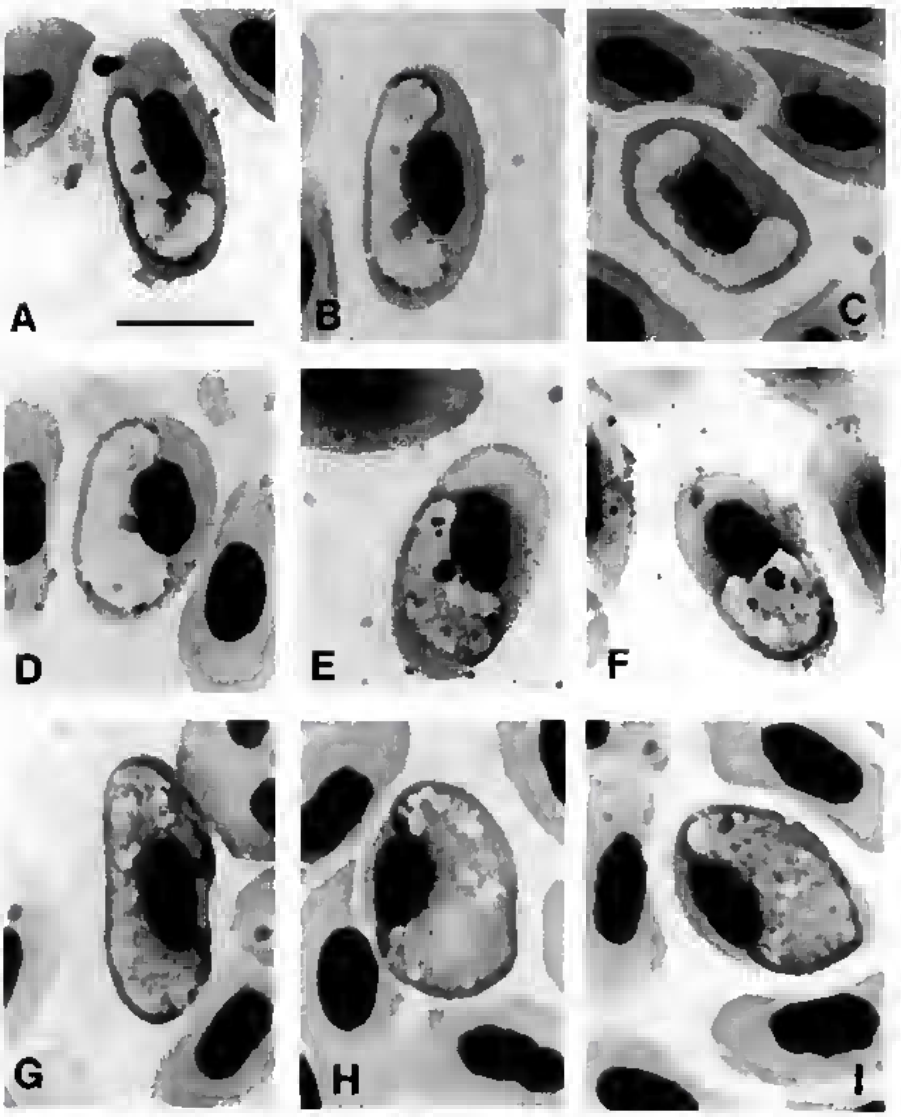


FIG. 17. — *Haemoproteus opluri* n. sp. : from hosts 234LL & 236LL ; A-E, microgametocyles ; F-I, macrogametocyles. Scale = 10 μm.

Data from 234LL and 236LL : Microgametocytes (figs. 17A-E, 18A, B) were usually oblong, 12,8-18,4 × 3,2-11,2 in size (m = 14,2 × 6,4 ; L/W 1,3-5,75, m = 2,7 ; n = 12), but a few were oval (10,4-13,6 × 9,6-11,2 ; L/W 1,1-1,2) (fig. 17F). The microgametocyte cytoplasm stained faintly blue-red, with faint outlines of vacuoles, and contained a deep red-staining whole or fragmented caryosome within a faint red nuclear zone, and in some cases accessory red granules. Fine pigment granules occurred mainly on the periphery. Macrogametocytes were halteridia-like (figs. 17G-I, 18C-F), 13,6-19,2 × 4,8-12,0 (m = 16,6 × 8,5 ; L/W 1,3-3,5, m = 1,97 ; n = 15). The blue-staining cytoplasm was of a foamy texture and contained a

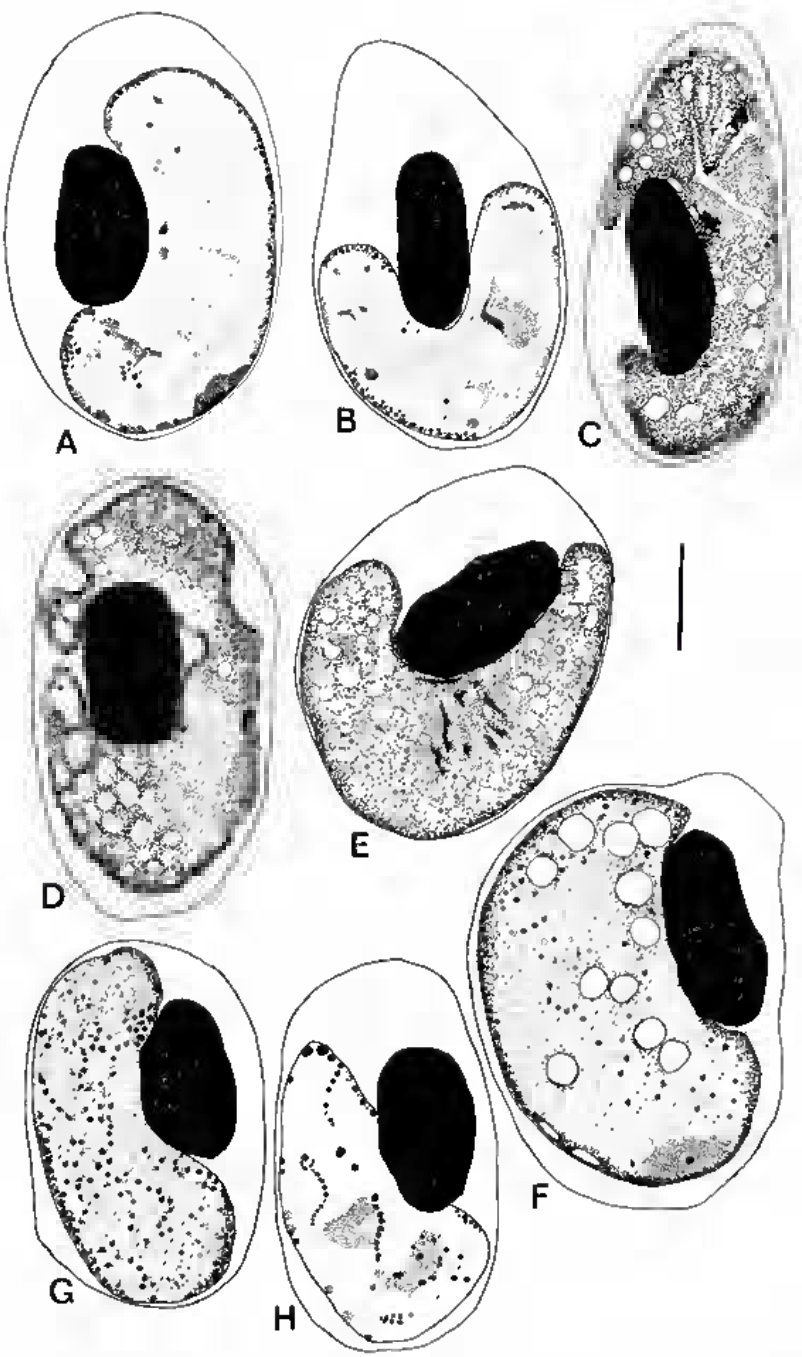


FIG. 18. — *Haemoproteus opluri* n. sp. : A-F from hosts 234LL, 236LL : A, B, microgametocytes; C-F, macrogametocytes; G, H, n from host 37LL : G, macrogametocyte; H, microgametocyte. Scale = 4 μm.

variable size, faintly outlined nuclear zone with a small or fragmented caryosome and a variable number of vacuoles. Fine pigment granules were scattered at random.

Data from 37LL : Microgametocytes 9,6-14,4 × 4,0-7,2, in size (m = 11,4 × 5,9; L/W 1,3-3,0, m = 2,0; n = 5) contained a larger concentration of coarse pigment granules (fig. 18H). Macrogametocytes were oblong and halteridia-like, 12,0-17,6 × 4,0-7,2 in size (m = 13,3 × 7,1; L/W 1,5-4,4, m = 2,2; n = 8), located alongside the RBC's nucleus, or oval, 10,4 × 9,6; 12,0 × 8,0; L/W 1,1; 1,5, in a polar position. The macrogametocyte's blue cytoplasm contained heavy concentration of pigment granules, while the nuclear element remained unstained (staining artefact?). Vacuoles were absent.

Effect on the host cells : In 234 and 236LL RBCs infected with microgametocytes usually retained their normal dimensions [16,8-21,6 × 8,8-12,0 (m = 18,6 × 10,6; n = 12) vs. normal RBC sizes of 15,2-20,8 × 8,0-10,4 (m = 19,3 × 9,4; n = 10)]. Oblong microgametocytes surrounded the centrally positioned RBC's nucleus, causing lateral expanding of the RBC in some. Oval microgametocytes were located at the polar end of the RBC, displacing its nucleus. RBC infected with macrogametocytes, similarly, retained their usual dimensions [16,0-20,8 × 8,8-12,8 (m = 18,2 × 10,6; n = 15)]. The oblong macrogametocytes were positioned alongside the nucleus. Very large specimens displaced the RBC's nucleus to marginal position, causing lateral expansion of the RBC (14,5 × 10-11). Some macrogametocytes completely enclosed the nucleus while displacing the entire cytoplasm. In 37LL, RBCs infected with microgametocytes and macrogametocytes were of somewhat reduced dimensions 14,4-19,2 × 8,8-12,8 (m = 16,1 × 10,4; n = 5); and 13,6-17,6 × 8,8-12,0 (m = 16,1 × 10,6; n = 8) in size respectively.

Levels of parasitaemia, multiple infections and sex ratio : In the three infected *O. cuvieri* 234LL, 236LL and 37LL, levels of parasitaemia were 0,2-0,4 %. Multiple infections were very rare. In Majunga lizards, there was a pronounced (1,8-2,75 : 1, in 234LL) or slight (1,1 : 1, in 236LL) dominance of microgametocytes. In the lizard from Belo sur Tsiribihina (37LL) microgametocytes were dominant (5,5 : 1).

Taxonomic evaluation

The nearly total absence of red stain in the microgametocyte cytoplasm, together with the very distinct appearance of the red-staining nuclear zone and the dense caryosome are unique features for this species. Fully developed macrogametocytes become very wide, contain several to many, very distinct large vacuoles, and fine granulated rather than coarse pigment. Among known species of reptilian *Haemoproteus* the only other species which possesses such combination of features is *H. oedurae*. The latter retains more pronounced halteridian characteristics, and shows a dense cytoplasm rather than the foamy one seen in this species. The distinct taxonomic status of the host (Opluridae) and its geographic location (Madagascar) further advocates the classification of this described *Haemoproteus* as a new species.

Differences between parasites seen in *O. cuvieri* from Majunga (234, 236LL) and from Belo sur Tsiribihina (37LL), mainly in size (but also in sex ratio) are likely to reflect differences between early and progressive stages of the infection. The invisibility of the nuclear zone in 37LL slides is apparently due to a fault or a degradation of the stain.

Haemoproteus cf. opluri
(Figs. 19, 20)

HOST : *Oplurus quadrimaculatus* A. Duméril, 1851.

LOCALITY : Fort Dauphin/Baie de Loukaro, Madagascar.

SPECIMENS : Slides deposited in the MNHN.

DESCRIPTION

Available blood smears only contained micro and macrogametocytes.

Microgametocytes were round or oval, 6,4-9,6 × 3,6-7,2 in size, L/W 1,0-2,6 (m = 8,2 × 5,9; L/W 1,6; n = 6), located at one end of the RBC (figs. 19A, 20D, E). The usually stain-resistant cytoplasm contained fine and coarse pigment granules, a scattered nuclear zone and, occasionally a caryosome. Young macrogametocytes (fig. 20A) were 4,0-4,8 × 2,4-4,0 in size, round, and their cytoplasmic components were identical to the larger macrogametocytes. The latter (figs. 19B-F, 20B, C, E) were round or oval, with occasionally undulating margins (fig. 20B), 8,0-12,0 × 6,4-8,8 in size, L/W 1,0-2,3 (m = 10,8 × 7,4; L/W 1,34; n = 21). One

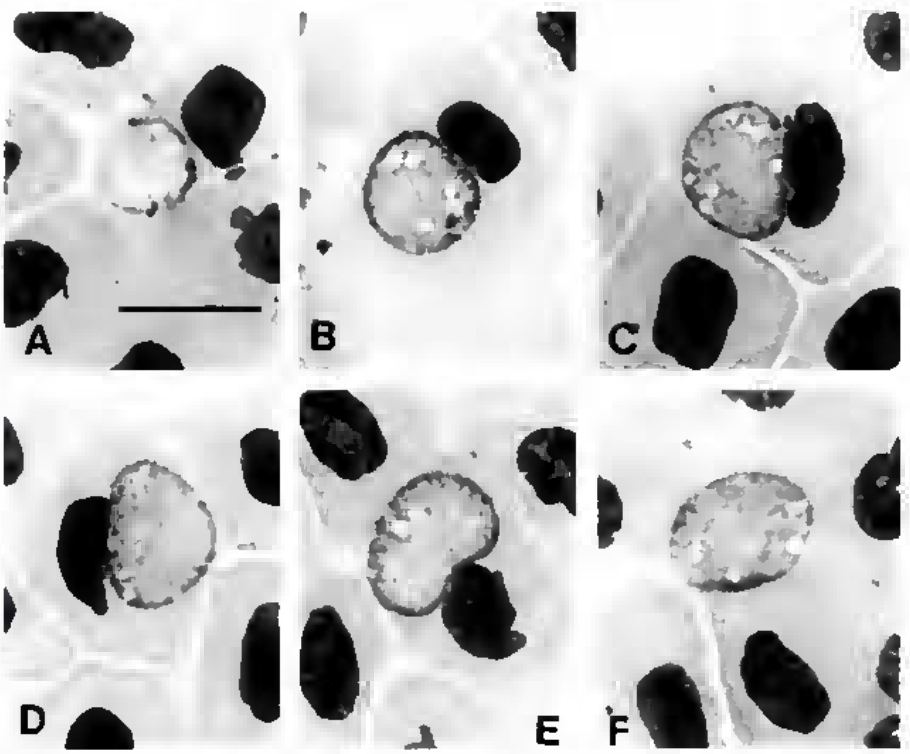


FIG. 19. — *Haemoproteus* cf. *opluri* : A, microgametocyte; B-F, macrogametocytes. Scale = 10 µm.

specimen (fig. 20B) was elongate (13,6 × 4,8; L/W 2,8). The foamy cytoplasm contained few vacuoles, scattered fine pigment granules and an extensive nuclear zone; caryosomes were not detectable. The macrogametocytes were either located alongside the nucleus (figs. 19C, D), or at one end of the RBC (figs. 19A, B, F).

Effect on the host cells : Uninfected RBCs were 16,8-20,0 × 8,8-12,8 in size (m = 18,9 × 10,8; n = 10). Infected RBCs remained about the same, when infected with microgametocytes : 17,0-21,6 × 8,8-12,0 (m = 19,2 × 9,7; n = 6), or macrogametocytes : 17,6-20,8 × 8,0-12,0 (m = 18,7 × 10,4; n = 13). Occasionally cells infected with gametocytes expanded laterally to a width of 12,8-14,4 (L/W 1,1-1,3).

Prevalence of infection, multiple infections and sex ratio : Level of parasitaemia varied within the range of 0,5 % to 1,3 %. Multiple infections seen once, with two juvenile macrogametocytes (fig. 20A). Macrogametocytes outnumbered microgametocytes by 2,6-11,0 : 1.

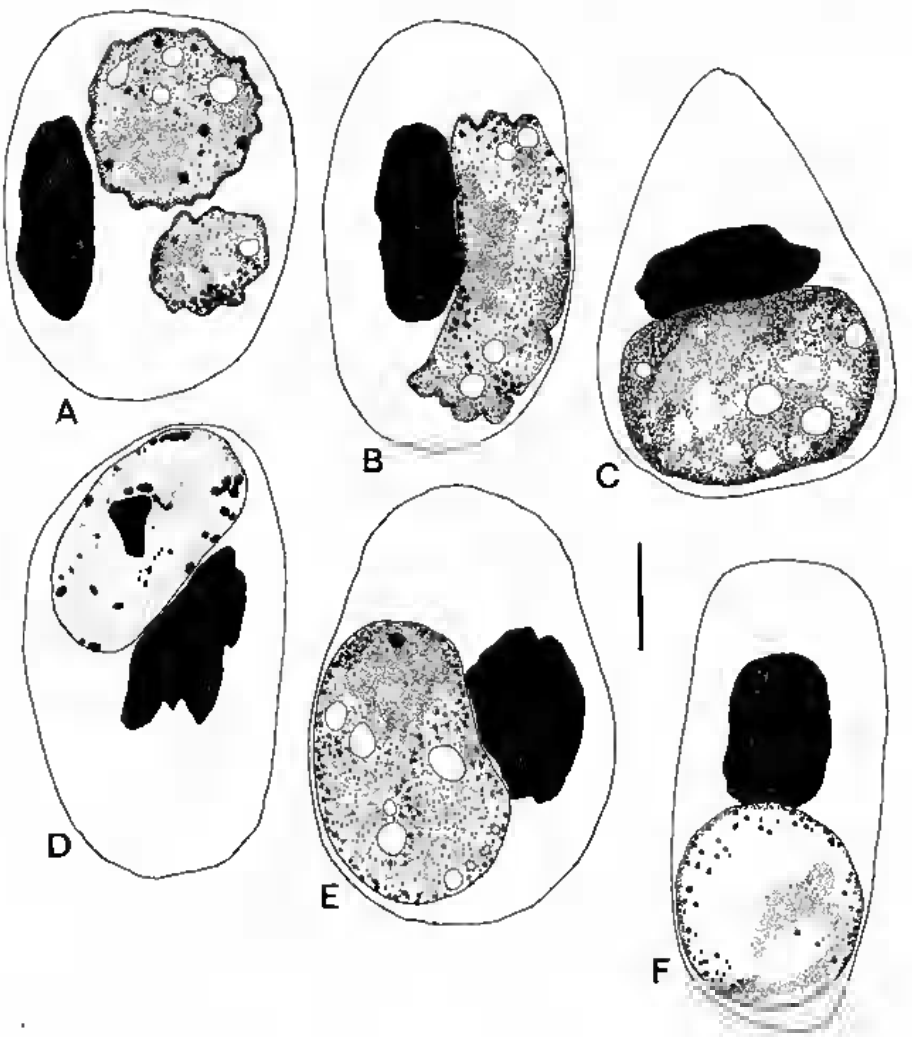


FIG. 20. — *Haemoproteus* cf. *opluri* : A, double infection by young macrogametocytes; B, C, E, macrogametocytes; D, F, microgametocyles. Scale = 4 µm.

Taxonomic evaluation

Both micro macrogametocytes closely resemble *H. opluri* in their cytoplasmic details. They differ mainly in size and in having a generally rounded shape. Also macrogametocytes numerically predominate microgametocytes while in *H. opluri* in two out of three of the hosts examined, microgametocytes outnumbered macrogametocytes.

Haemoproteus from *O. cuvieri* and *H. quadrimaculatus* seem to be conspecific. The differences listed above could be the result of specimens being at an earlier stage of infection, or of a different level of compatibility with the host, causing the formation of smaller mature gametocytes.

DISCUSSION

Criteria for specific differenciation

Gametocytes' size and position in the RBC host cell is used for differentiating species of avian *Haemoproteus* (Bennet & Campbell, 1972). In some species of saurian hemoproteids, shape (oval or halteridian) and position within the RBC are a variable, while in others it is an invariable characteristic. Other characteristics employed for species differenciation are the pattern of the pigment distribution, number and dispersal of vacuoles and vesicles and stainability of nuclear organelles. All these characteristics may differ in micro and macrogametocytes (examples ; *H. kopki*, de Mello, 1916, Telford, 1982; *H. underwoodsauri*, *H. edomensis*, present study) and may change with the gametocyte age (maturation or senility, example : *H. tarentolae*, present study). Differential diagnosis preferably should analyze data from a population, comprised of premature and mature of both micro and macrogametocytes. Staining as well as pigment composition was found sometimes to deteriorate in stored museum slides.

Course of infection and sex ratios seem to be equally important differential characteristics as structural affinities. Among the *Haemoproteus* species studied here, there was a clear, interspecific variability in the production rate of young gametocytes (i.e. recrudescence of blood gametocytes) as well as in the prevalence of multiple infections in the RBC. In some species recruitment of juveniles was limited to the early period of the infection only (*H. underwoodsauri*, *H. ptyodactyli*, *H. opluri* and apparently also *H. simondi*) or occurred intermittently throughout the period of parasitaemia (*H. gehyrae*, *H. tarentolae*). In others, it was continuous, persisting throughout the period of the parasitaemia (*H. edomensis*), or at least throughout the period of high parasitaemia (*H. oedurae* and apparently also *H. mackerrasi*).

Multiple infections appear to be parasite density-dependent and therefore also coincided with active juvenile recruitment (in *H. oedurae*, *H. edomensis*). However, their rarity or complete absence in some species (*H. ptyodactyli*, *H. opluri*) and their permanent abundance in

others (*H. simondi, H. mackerrasi, H. gehyrae*) might be regarded as a species characteristic. Interspecific variations with respect to presence or rarity/absence of multiple infections were evident in the genus *Fallisia* (LAINSON, SHAW & LANDAU, 1974; TELFORD, 1986; PAPERNA & LANDAU, 1990).

There is a characteristic disparity between micro and macrogametocytes which is maintained throughout the greater part of the course of infection in the blood. In most species microgametocytes were predominant throughout the observation period or most of it. The exceptions were *H. simondi, H. tarentolae* and *H. edomensis*, where macrogametocytes were dominant. Sex ratios were variable only in *H. opluri*, but our follow-up period was very short. Data on sex ratios among gametocytes of other haemospidia other than from reptiles are scarce; in the saurian plasmodiids : *Plasmodium mexicanum, P. agamae* and *P. giganteum*, and in *Fallisia effusa* and *F. copemani* macrogametocytes were dominant (LAINSON, SHAW & LANDAU, 1975; SCHALL, 1989; PAPERNA & LANDAU, 1990).

Generic status

Haemoproteid parasites of mammals were given separate generic status from those from avian and reptilian hosts (GARNHAM, 1966). Haemoproteids of avian hosts are divided between two genera : *Haemoproteus* and *Parahaemoproteus*, differentiated from each other by their specific vectors and the nature of their exoerythrocytic stages (GARNHAM, 1966).

Data on developmental stages of reptilian haemoproteids, other than the intraerythrocytic, are available only on *H. metchhnikovi* — exoerythrocytic stages (STERLING & DE GIUSTI, 1972) and developmental stages in the vector (DE GIUSTI, STERLING & DOBRZECHOWSKI, 1973), and on the exoerythrocytic stages of *H. simondi* (SHORTT, 1962). These data are insufficient to offer enlightenment as to the taxonomic affiliations of reptilian haemoproteids with the genus *Haemoproteus* (s. str.), or to support any generic definition of reptilian haemoproteids.

Haemoproteids of lacertilian reptiles were segregated into a separate genus *Haemocystidium* Castellani & Willey, 1904. Into this genus JOHNSTON & CLELAND (1909) also included haemoproteids described from a chelonian host in Australia (*H. chelodinae*). WENYON (1926) moved the reptilian haemoproteids to the genus *Haemoproteus*, while MACKERRAS (1961) and GARNHAM (1966) returned to the use of *Haemocystidium* for species from reptilian hosts. GARNHAM (1966) also created a new genus, *Simondia*, for haemoproteids of chelonians.

The main characteristic used to differentiate *Haemocystidium* from *Haemoproteus* : the oval rather than halteridium-like gametocyte (CASTELLANI & WILLEY, 1904; SHORTT, 1922; MACKERRAS, 1961) is a persistant characteristic only in part of the reptilian haemoproteids, in the rest, oval gametocytes occur concurrently with halteridial ones, and there are also species which form exclusively halteridial gametocytes. Moreover, in some species, for example *H. underwoodsauri*, one sex gametocytes are oval while the other sex gametocytes are halteridian.

LIST OF HAEMOPROTEID SPECIES FROM SQUAMOUS REPTILES

GECKOES, AUSTRALIA : *H. mackerrasi* n. sp.; *H. gehyrae* n. sp; *H. oedurae* n. sp.; *H. underwoodsauri* n. sp.

GECKOES, MEDITERRANEAN : *H. tarentolae* (Parrot, 1927); *H. ptyodactyli* n. sp.

GECKOES, INDO-IRAN : *H. simondi* (Castellani & Willey, 1904); *H. kopki* (de Mello, 1916); *H. phyllodactyli* Shortt, 1922.

AGAMID LIZARDS, EAST MEDITERRANEAN-IRANO-TURKESTAN : *H. grahmi* Shortt, 1922; *H. edomensis* n. sp.

AGAMID LIZARDS, AFRICA : *H.* spp. of MACFIE, 1914; of BRAY, 1959; of BALL, 1967.

ENDEMIC LIZARDS, MADAGASCAR : *H. opluri* n. sp; *H.* cf. *opluri.*

SNAKES, AFRICA : *H. mesnili* (Bouet, 1909); *H. najae* (Wenyon, 1909).

Aknowledgemeots

We wish to thank Drs Bruce COPEMAN of the Graduate School for Tropical Veterinary Sciences at James Cook University of North Queensland and Peter J. O'DONOGHUE of the Central Veterinary Laboratories, Adelaide, South Australia, for their hospitality and support of our field work in Australia; Dr Steve DONELLAN, South Australia Museum, for his help in collecting reptiles and their identification; Prof. J. A. RIOUX, Laboratoire d'Écologie médicale et de Pathologie parasitaire, Faculté de Médecine, Montpellier, for his support, and Ms E. GUILVARD for instructing and helping in the feeding experiments with *Phlebotomus papatasi.*

REFERENCES

BALL, G. H., 1967. — Some blood sporozoans from east African reptiles. *J. Protozool.*, **14** : 198-210.

BENNETT, G. F., & A. G. CAMBELL, 1972. — Avian Haemoproteidae. 1. Description of *Haemoproteus fallisi* n. sp. and a review of the haemoproteids of the family Turdidae. *Can. J. Zool.*, **50** : 1269-1275.

BOGDANOV, O. P., G. S. MARKOV & N. M. RADCHENKO, 1970. — Blood parasites in Turkestanian agama. *In* : Questions on morphology, ecology and parasitology of animals Volgograd, p. 105-111 (in Russian).

BOUET, J., 1909. — Sur deux hèmocytozoaires pigmentés des reptiles. *C. r. Sèanc. Soc. Biol.*, **66** : 33-48.

BRAY, R. S., 1959. — On the parasitic protozoa of Liberia. II. The malarial parasites of agamid lizards. *J. Protozool.*, **6** : 13-18.

CASTELLANI, A., & A. WILLEY, 1904. — Observations on the hematozoa of vertebrates in Ceylon. *Spolia zeylan.*, **2** : 78-92.

DE GIUSTI, D. L., C. R. STERLING & D. DOBRZECHOWSKI, 1973. — Transmission of the chelonian haemoproteids *Haemoproteus metchnikovi* by a tabanid fly, *Chrysops callidus*. *Nature*, **242** : 50-51.

DE MELLO, F., 1916. — Quelques considérations sur les affinités zoologiques du genre « *Haemocystidium* » avec description d'une espèce nouvelle. *Anais Fac. Med. Porto*, **3** (1).

DOBELL, C. C., 1910. — Contributions to the life history of *Haemocystidium simondi* Castellani & Willey. *Festschr. 60 Geburst, R. Hertwigs*, **2** : 124-132.

GARNHAM, P. C. C., 1966. — Malaria parasites and other Haemosporidia. Blackwell Sci. Publ., Oxford.

ITURBE, J., & E. GONZALEZ, 1921. — Sobre algunos datos de protozoologia y parasitologia recogidos en San Juan de los Morros *Gac. méd. Caracas*, **28** : 275-283.

JONHSTON, T. H., & J. B. CLELAND, 1909. — On a new melanin-producing hematozoon from an Australian tortoise. *J. roy. Soc. N. S. W.*, **43** : 97-193.

LAINSON, R., I. LANDAU & J. J. SHAW, 1974. — Further parasites of the family Garniidae (Coccidiida : Haemosporidiidea) in Brazilian lizards. *Fallisia effusa* gen nov., sp. nov. *Parasitology*, **68** : 117-125.

LAINSON, R., J. J. SHAW & I. LANDAU, 1975. — Some blood parasites of the Brazilian lizards *Plica umbra* and *Uranoscodon superciliosa* (Iguanidae). *Parasitology*, **70** : 119-141.

MACFIE, J. W. S., 1914. — Note on some blood parasites collected in Nigeria. *Ann. trop. Med. Parasitol.*, **8** : 439-468.

— 1919. — Two parasites of *Naja nigricollis*. *Ann. trop. Med. Parasitol.*, **13** : 23-30.

MACKERRAS, M. J., 1961. — The haematozoa of Australian reptiles. *Aust. J. Zool.*, 9 : 61-122.

OVEZMUKHAMEDOV, A., 1987. — Protistofauna of reptiles. Ed. Berdiev A., « Ilim », Ashkabad Turkeman S.S.R., 373 p. (in Russian).

PAPERNA, I., & I. LANDAU, 1990. — *Fallisia copemani* n. sp. (Haemosporidia : Garnidae) from the Australian skink *Carlia rhomboidalis*. *Ann. Parasitol. hum. comp.*, **65** : 16-21.

PAPERNA, I., & I. LANDAU, 1990. — *Billbraya australis* n. g., n. sp. from the South Australian gecko *Phyllodactylus marmoratus*. *Ann. Parasitol. hum. comp.*, **65** : 170-176.

PARROT, L., 1927. — Sur un parasite intraglobulaire pigmenté de *Tarentola mauritanica* (L.). *Arch. Inst. Pasteur Algér.*, **5** : 1-8.

PESSOA, S. B., & J. CAVALHEIRO, 1970. — Sobre uma nova especie de *Haemoproteus*, parasita de uma lagartixa, *Enyolius catenatus* (Wied, 1821) de Sao Paulo (Brasil). *Revta bras. Biol.*, **30** : 403-404.

RIDING, D., 1930. — *Haemoproteus* of *Tarentola annularis*. *Trans. R. Soc. trop. Med. Hyg.*, **23** : 635-636.

SCHALL, J. J., 1989. — The sex ratio of *Plasmodium* gametocytes. *Parasitology*, **98** : 343-350.

SHORTT, H. E., 1922. — Review of the position of the genus *Haemocystidium* (Castellani & Willey, 1904), with a description of two new species. *Indian J. med. Res.*, 9 : 814-826.

— 1962. — Exo-erythrocytic schizont of *Haemoproteus*, parasite of the gecko *Hemidactylus* sp. in the liver. *Trans. R. Soc. trop. Med. Hyg.*, **56** : 3.

STERLING, C. R., & D. L. DE GIUSTI, 1972. — Ultrastructural aspects of schizogony, mature schizonts and merozoites of *Haemoproteus metchnikovi*. *J. Parasitol.*, **58** : 641-652.

STERLING, C. R., & D. L. DE GIUSTI, 1974. — Fine structure of differentiating oocysts and mature sporozoites of *Haemoproteus metchnikovi* in its intermediate host *Chrysops callidus*. *J. Protozool.*, **21** : 276-283.

TELFORD, S. R., Jr., 1982. — Re-discovery of *Haemoproteus kopki* (De Mello, 1916) in two geckoes from the Afghan border of Pakistan. *Parasitology*, **84** : 527-536.

— 1984. — Haemoparasites of reptiles. *In* : Diseases of Amphibians and Reptiles, Ed. G. L. Hoff, F. L. Frye & E. R. Jacobson, Plenum Press N.Y., p. 285-517.

WENYON, C. M., 1909. — Report of the travelling pathologist and protozoologist. *Rep. Wallcome trop. Res. Lab.*, n° 3 : 121-168.

— 1915. — The pigmented parasites of cold-blooded animals, with some notes on a *Plasmodium* of the Trinidad iguana. *J. trop. Med. Hyg.*, **18** : 133-140.

— 1926. — Protozoology. Baillière, Tindall & Cox, London.